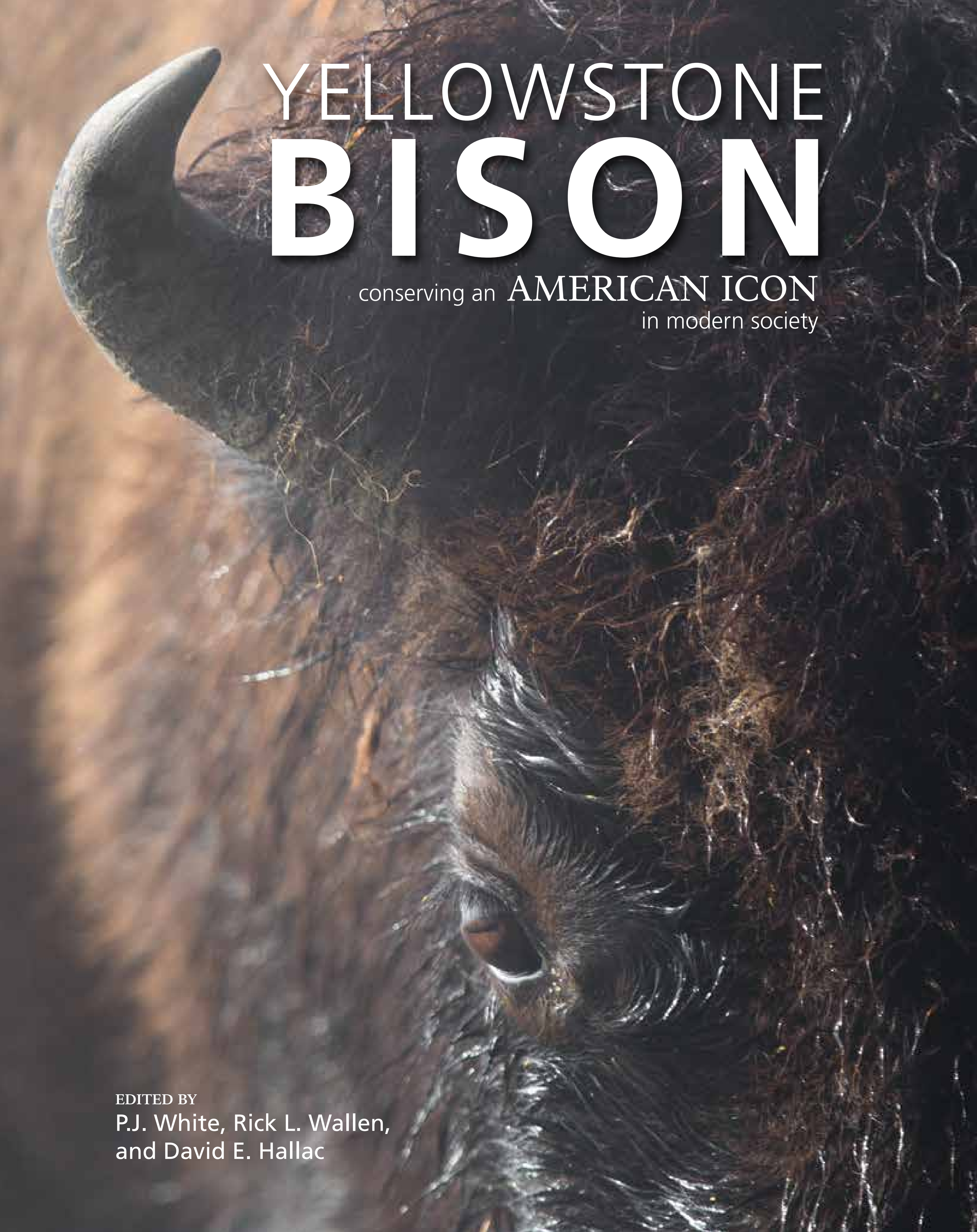

# YELLOWSTONE BISON

## conserving an AMERICAN ICON in modern society

EDITED BY
P.J. White, Rick L. Wallen, and David E. Hallac

YELLOWSTONE BISON

# Yellowstone Bison: Conserving an American Icon in Modern Society

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Yellowstone Association    Yellowstone National Park, USA, 2015

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The Yellowstone Association, Yellowstone National Park 82190
Published 2015
Printed in the United States of America



Library of Congress Cataloging-in-Publication Data
Yellowstone bison : conserving an American icon in modern society / edited by P.J. White, Rick L. Wallen, and David E. Hallac ; contributing authors, Katrina L. Auttelet [and 10 others] ; contributing editor, Jennifer A. Jerrett.
pages cm
Includes bibliographical references and index.
ISBN 978-0-934948-30-2 (pbk. : alk. paper)
1. American bison--Conservation--Yellowstone National Park. 2. American bison--Conservation--United States. 3. Wildlife conservation--Yellowstone National Park. 4. Wildlife conservation--United States. 5. Wildlife management--Yellowstone National Park. I. White, P. J. (Patrick James) II. Wallen, Rick L. III. Hallac, David E. IV. Auttelet, Katrina L. V. Jerrett, Jennifer A.
QL737.U53Y45 2015
599.64'30978752--dc23
2015004628

The authors gratefully acknowledge the generous contribution of the Yellowstone Association, whose publication grant enabled the production of this book.

# Contents

Abbreviations used in citations:

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| APHIS | Animal and Plant Health Inspection Service |
| MDOL | Montana Department of Livestock |
| MFWP | Montana Fish, Wildlife & Parks |
| NPS | National Park Service |
| USDA | United States [U.S.] Department of Agriculture |
| USDI | U.S. Department of the Interior |
| USFS | U.S. Forest Service |
| YNP | Yellowstone National Park |

Recommended citation format:

Entire book.—White, P. J., R. L. Wallen, D. E. Hallac, and J. A. Jerrett, editors. 2015. Yellowstone bison—Conserving an American icon in modern society. Yellowstone Association, Yellowstone National Park, Wyoming.

Individual chapter.—Wallen, R. L., P. J. White, and C. Geremia. 2015. Historical perspective. Pages 45-65 in P. J. White, R. L. Wallen, D. E. Hallac, and J. A. Jerrett, editors. Yellowstone bison—Conserving an American icon in modern society. Yellowstone Association, Yellowstone National Park, Wyoming.


*Bison in winter, Yellowstone National Park.*

# Preface

*Daniel N. Wenk, Superintendent, Yellowstone National Park*

My association with bison management in Yellowstone National Park began in the early 1980s when I worked for Superintendents John Townsley and Bob Barbee. Back then, there were fewer than 2,500 bison and the central herd was the largest herd in the park. Also, bison were not yet making seasonal migrations past the north and west boundaries of the national park. Because bison were not leaving the park, brucellosis within the population was less of a concern. Bison contributed greatly to the enjoyment of the park by visitors as part of the incredible wildlife display.

Much has changed. About three decades later, when I was preparing to return to the park as Superintendent beginning February of 2011, I was made aware of a court-mediated settlement regarding the management of bison signed by the Secretaries of Agriculture and the Interior and the Governor of Montana. But my knowledge came from a distance, and I did not yet fully understand or appreciate the complexity of management or the intensity of emotion and conflict that was occurring on the boundaries of Yellowstone National Park.

My education came quick. The winter of 2010-2011 was harsh and bison were moving into the Gardiner basin of Montana in large numbers. Within two weeks of my arrival in the park, I was in Montana Governor Brian Schweitzer's office in the state capital to discuss bison management. The Governor suggested methods to control population numbers and brucellosis, including a proposal to hunt bison within the national park. I rejected this proposal because it was contrary to law, regulation, and policy of the National Park Service and Yellowstone. It was also unnecessary; the park could ecologically support the bison population and we were successfully managing the population without hunting in the park.

In an unexpected turn of events, and what would become my first lesson in the politics of bison management, Governor Schweitzer issued an Executive Order prohibiting the shipment of bison on state highways. The hands of the National Park Service were tied. That winter, approximately 850 bison were held in capture facilities until early May when they migrated back into the park.

What I learned in my first weeks as Superintendent is that the science, so well-highlighted in this book, must be joined with the strength and commitment of people to successfully manage a wide-roaming bison population and prevent brucellosis transmission to cattle. Many of these individuals are the authors of this book: wildlife biologists, law-enforcement officers, and others who are the experts in the field of bison management. Herein, they clearly articulate not only the science, but also, the cultural and political significance of bison management.

During my time in Yellowstone, I have watched with great interest—and some amazement—that bison are vilified as the primary threat or vector for brucellosis transmission in the ecosystem. There is an illusory belief that if brucellosis were eliminated in bison it would be eliminated from the ecosystem. The authors show clearly that this scenario is unlikely, and that bison make up a small portion of the overall risk for brucellosis transmission to cattle.

Bison are a wildlife icon in America, and Yellowstone bison represent one of the greatest wildlife conservation stories in our nation's history.

The authors provide a compelling history of the conservation of bison from the early 1900s to the management of bison in modern society. This book is based on the best available science, understanding the importance of bison in the American Indian culture, understanding brucellosis and the role bison play in the ecology of the Greater Yellowstone Area, and an understanding of the stakeholders and local community issues. It informs our collective management and commitment to wild bison on the landscape.

The iconic bison deserves our best efforts to assure its place on the American landscape. I am grateful to the authors for clearly articulating the issues we face as we collectively determine the future of these animals. The authors have given us a chance to advance our discussions based on a common understanding of the science, culture, and politics surrounding bison.


*Clouds and bison across Hayden Valley, Yellowstone National Park.*

# Introduction

*P.J. White, Rick L. Wallen, and David E. Hallac*

The plains bison (*Bison bison* or *Bos bison*), also commonly known as buffalo, once numbered in the tens of millions and ranged across much of North America, from arid grasslands in northern Mexico, through the Great Plains and Rocky Mountains into southern Canada, and eastward to the western Appalachian Mountains (Lott 2002; Gates et al. 2010; Bailey 2013). Plains bison are symbolic of the American experience because they are an inherent part of the cultural heritage of many American Indian tribes and were central to national expansion and development (Plumb and Sucec 2006). Only a few hundred plains bison survived commercial hunting and slaughter during the middle to late 1800s, with the newly established (1872) Yellowstone National Park providing refuge to a relict, wild, and free-ranging herd of less than 25 animals (Meagher 1973). This predicament led to one of the first movements to save a species in peril and develop a national conservation ethic by a few visionary individuals, American Indian tribes, the American Bison Society, the Bronx Zoo, and federal and state governments (Plumb and Sucec 2006). Bison numbers increased rapidly after protection from poaching, reintroduction to various locations, and husbandry (see Glossary of Terms). Today, more than 400,000 plains bison live in conservation and commercial herds across North America (Coder 1975; Boyd 2003; Plumb and Sucec 2006; Freese et al. 2007; Hedrick 2009).

Despite this success, several scientists recently concluded that plains bison are ecologically extinct because less than 4 percent (20,000) are in herds managed for conservation and less than 2 percent (7,500) have no evidence of genes from inter-breeding with cattle (Freese et al. 2007). Most bison are raised for meat production, mixed with cattle genes, protected from predators, and fenced in pastures (McDonald 2001; Lott 2002; Freese et al. 2007; Sanderson et al. 2008; Gates et al. 2010; Bailey 2013). As a result, wild bison no longer influence the landscape on the vast scale of historical times by enhancing nutrient cycling, competing with other ungulates, creating wallows and small wetlands, converting grass to animal matter, and providing sustenance for predators, scavengers, and decomposers (Knapp et al. 1999; Lott 2002; Freese et al. 2007; Sanderson et al. 2008; Bailey 2013).

The restoration of wild bison has advanced more slowly, and with much greater debate, than nearly all other wildlife species over the past 150 years (Lott 2002; Bailey 2013). Bison are massive animals that compete directly with humans and livestock for use of the landscape (Boyd 2003). Their preferred habitats include nutrient-rich valley bottoms where agricultural and residential developments occupy most of the land, while public lands are more likely to encompass mountainous areas (Scott et al. 2001; Becker et al. 2013). Given existing habitat loss and the constraints modern society has placed on the distribution of wild bison, it is unlikely many additional populations will be established and allowed to roam widely across the landscape (Lott 2002; Boyd 2003). Thus, the few remaining wild and wide-ranging populations of plains bison in the Greater Yellowstone Area (Jackson and Yellowstone populations), Canada (Pink Mountain, British Columbia and Prince Albert National Park), and Utah (Book Cliffs and Henry Mountains) are very important (Keiter and Boyce 1991; Franke 2005; Plumb et al. 2009; White and Wallen 2012; Bailey 2013).

In 1973, Dr. Mary Meagher, a research biologist working in Yellowstone National Park, released a scientific monograph that provided insightful information on the life history, behaviors, and ecology of Yellowstone bison. This work was invaluable to biologists that managed bison during subsequent decades, and much of it is still pertinent and has been referenced in this book. During the past 40 years, however, there have been significant advances in understanding bison ecology, and also, substantial changes in the abundance, distribution, movements, and management of Yellowstone bison (Plumb et al. 2009; Gates and Broberg 2011; White et al. 2011, 2013b; White and Gunther 2013). In addition, there are biological, political, and social threats to Yellowstone bison that hinder their conservation and the recovery of the species elsewhere (Franke 2005; Plumb et al. 2009; Bailey 2013; Treanor et al. 2013; White et al. 2013a).

This book provides updated information on Yellowstone bison. We compiled information from numerous published and unpublished sources (e.g., articles, environmental compliance documents, newspapers, reports, websites) not readily available to many stakeholders. We reorganized this information into a more concise and readable format, without detailed data collection methods and statistical analyses. However, the original sources of information are cited and the wording is often similar to preserve original intent and avoid misrepresentation.

In the book, we discuss opportunities for bison conservation in the Yellowstone area, misconceptions and competing social values that prevent an easy path forward for bison conservation, and the potential for Yellowstone bison to contribute to the conservation of plains bison across their historic range. Our objectives are to communicate this information to natural resource managers, wildlife ecologists, and anyone interested in plains bison so they can work together to enhance the conservation of this species in modern society. Also, we hope this information will benefit the millions of people that visit Yellowstone National Park each year or monitor the condition and management of the park's resources via the Internet or other outreach avenues.


*Bull bison in the Pelican Valley of Yellowstone National Park.*

# Chapter 1

## THE POPULATION—ATTRIBUTES, BEHAVIOR, DISTRIBUTION, RESOURCE USE, AND TRENDS

*Douglas W. Blanton, P.J. White, Rick L. Wallen, Katrina L. Auttelet, Angela J. Stewart, and Amanda M. Bramblett*

YELLOWSTONE BISON ARE noteworthy in modern times because, unlike most other conservation herds, this population has thousands of individuals that roam relatively freely over an expansive landscape (Franke 2005; Freese et al. 2007; Bailey 2013). They also exhibit wild behaviors reminiscent of prehistoric populations, with large congregations of individuals during the breeding season to compete for mates, as well as migration and pioneering movements to explore new areas (Plumb et al. 2009; Gates and Broberg 2011; Geremia et al. 2011, 2014b). These behaviors contributed to the successful restoration of a population that was on the brink of extinction just over a century ago (Plumb and Sucec 2006; Plumb et al. 2009).

## Attributes

Plains bison are massive animals, with males (900 kilograms or 1,985 pounds) having larger maximum weights than females (500 kilograms or 1,100 pounds; Meagher 1986). Males are full-grown by 5 to 6 years of age, while females mature near 3 years of age (Meagher 1986). Yearlings weigh 225 to 320 kilograms (500 to 700 pounds), while calves 8 to 9 months old weigh 135 to 180 kilograms (300 to 400 pounds; Meagher 1973; Gogan et al. 2010). Adult bison are dark chocolate-brown in color, with long hair (15 centimeters or 6 inches) on their forelegs, head, and shoulders, but short dense hair (3 centimeters or 1 inch) on their flanks and hindquarters (Meagher 1986). The fur of newborn calves is reddish tan in color, but begins turning brown at about 2.5 months (Meagher 1986). Both sexes have two horns that curve upward from their head and are retained for their lifespan. Horns of adult males in Yellowstone average about 36 centimeters (14 inches) in length, while those of adult females average about 31 centimeters (12 inches).[1]

All plains bison have a shoulder hump that extends to about 1.8 meters (6 feet) above-ground in adult males and 1.5 meters (5 feet) above-ground in adult females (Meagher 1986). Bison use their large shoulder and neck muscles to swing their heads from side-to-side to clear snow from foraging patches (Picton 2005). Bison get their first permanent incisor during their third year of life and gain teeth every year thereafter until they have a full set of permanent teeth at age five (Fuller 1959). Bison are agile, strong swimmers, and can run 55 kilometers (35 miles) per hour (Meagher 1973, 1986). They can jump over objects about 1.8 meters (6 feet) tall and have excellent hearing, vision, and sense of smell (Meagher 1973; Lott 2002).

## Social Behavior

Yellowstone bison are gregarious and often form female-led groups consisting of females of all ages and young males less than 4 years old. Group formation and dispersion is flexible, with the exception of a mother and her calf (Lott and Minta 1983; Lott 2002). Group sizes in Yellowstone

1 Portions of this chapter and other portions of the book have been included in and/or adapted from briefs, letters, websites, the Yellowstone Resources and Issues Handbook, and other National Park Service documents.


*Bison near Wraith Falls in the northern region of Yellowstone National Park.*

National Park average about 20 bison during winter (maximum = 175) and 200 bison (maximum = 1,000) during the summer breeding season from mid-July to mid-August. Group sizes decrease through autumn (average = 50 to 100 bison; maximum = 250 to 450) and reach their lowest level during winter in March and April (U.S. Department of the Interior [USDI[2]], National Park Service [NPS] 2010). The gregarious nature of bison tends to hold groups together, but their movements result in groups frequently encountering each other and intermixing to some extent (Lott 2002).

*Yellowstone bison are noteworthy in modern times because, unlike most other conservation herds, this population has thousands of individuals that roam relatively freely over an expansive landscape.*

The strongest relationships in plains bison society are between adult females and their calves, which are dependent on their mothers for food and security during their first three months of life (Lott 2002). Thereafter, calves suckle less and begin to procure food by grazing (Green 1992). When breeding begins, calves spend more time away from their mothers interacting with other bison approximately their own age (Green et al. 1989; Green 1992). However, most calves stay near their mothers for about one year (Lott 2002). Older and larger female bison often use threatening postures and pushing to establish dominance over unrelated younger or smaller animals, but actual fights are rare. Dominant females often displace other bison from feeding craters dug into the snow pack when food is limited during winter.

Adult bison form courtship groups in the Hayden and Lamar valleys of Yellowstone National Park during July and August (Meagher 1973). Plains bison reach sexual maturity at 2 to 4 years of age, but males usually do not successfully breed until about 6 years due to the presence of larger, older males (Meagher 1986; Berger and Cunningham 1994). Mature males fight to determine dominance, with competitive interactions including threatening postures, growling-type vocalizations, and sometimes, violent head-to-head clashes with opponents pushing to displace each other (McHugh 1958; Berger and Cunningham 1994). Winners have an opportunity to copulate with receptive females, and as few as 10 percent of the males in the population may complete 50 percent of the breeding during a given year (McHugh 1958, 1972; Berger and Cunningham

2 Abbreviations for government agencies frequently referenced in citations are provided after the Table of Contents

1994; Halbert et al. 2004). Following breeding, mature males segregate and spend the rest of the year alone or in small groups (McHugh 1972; Meagher 1973; Lott 2002). More information on bison reproduction can be found in Chapter 5.

Yellowstone bison employ a predator defense strategy whereby bison in a group cooperate to defend themselves and their young (Smith et al. 2000; MacNulty et al. 2007; Becker et al. 2009a). When threatened by predators such as wolves (*Canis lupus*), bison often gather together around young animals. Older males and females may challenge the predator(s), with their heads down and horns ready to hook their opponents. If one bison becomes vulnerable or is attacked, other bison may engage the predator(s) from a different direction. Bison usually prevail against one or a few predators when they employ this group defense strategy (MacNulty et al. 2007). More information on predation and mortality of bison can be found in Chapter 5.

## Habitats and Distribution

Historically, bison occupied about 20,000 square kilometers (7,720 square miles) near the sources of the Yellowstone and Madison rivers (Schullery and Whittlesey 2006). Today, this range is restricted primarily to the northern and central regions of Yellowstone National Park and adjacent areas in Montana (Figure 1.1). Few bison currently migrate from the park into adjacent areas of Idaho and Wyoming. Within this range, Yellowstone bison use a variety of habitats, including sedge meadow, upland, burned and unburned forest, sub-alpine, creek/river riparian areas, willow, and agricultural land outside the park (Meagher 1973; Jerde et al. 2001; Gross et al. 2010). Also, much of central Yellowstone is influenced by heat flowing to the surface from the interior of the Earth (Watson et al. 2009). This heat produces hydrothermal features such as geysers, hot springs, fumaroles, and mud pots in some areas, but also warms more extensive portions of the landscape where snow pack is reduced or eliminated (Watson et al. 2009). These geothermally influenced areas are often used by bison during winter (Meagher 1973; Bruggeman et al. 2009c).

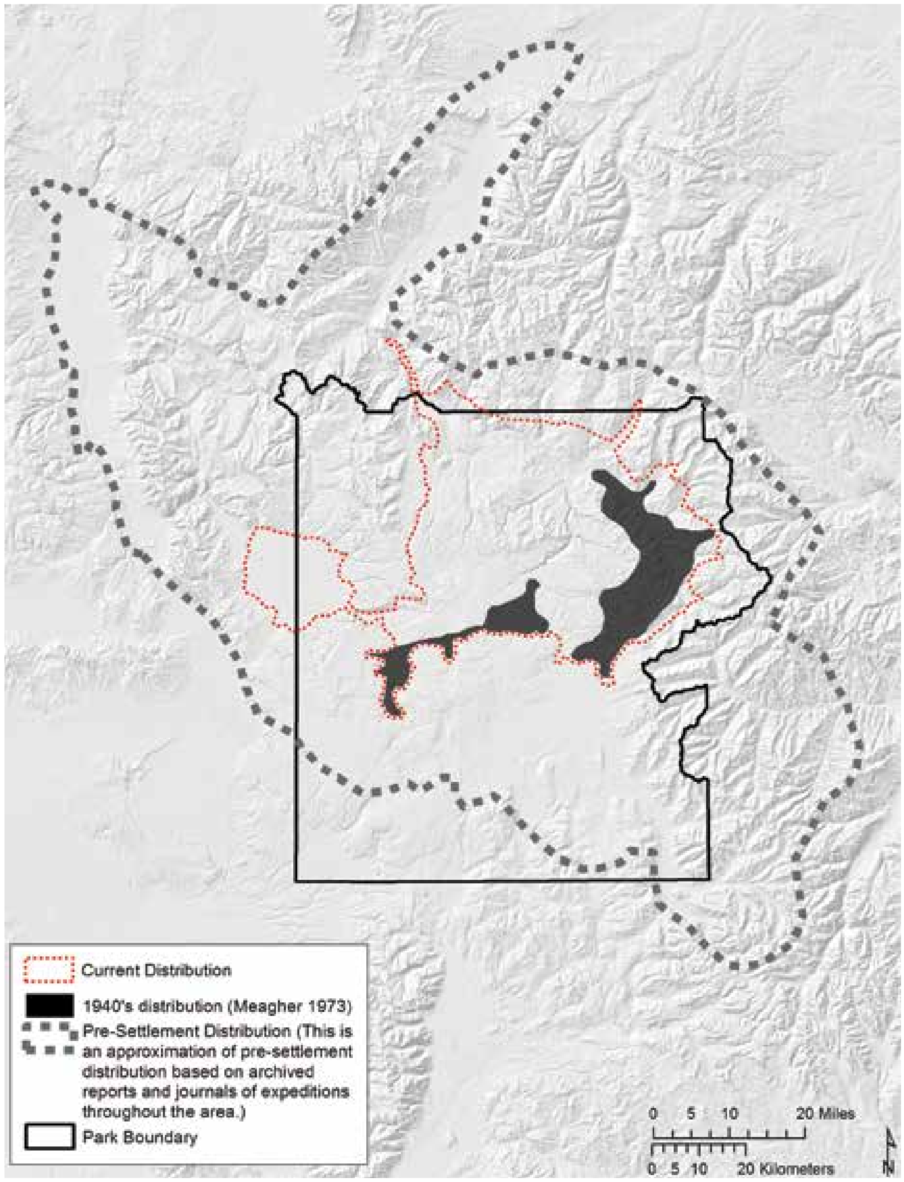


*Figure 1.1. Map depicting Yellowstone National Park and the pre-settlement, mid-20th century, and 2014 distribution of Yellowstone bison (adapted from Plumb et al. 2009). This figure does not depict the historic or current distribution of plains bison in and near Grand Teton National Park, the National Elk Refuge, or Jackson Hole, Wyoming.*

Bison in central Yellowstone occupy the central plateau, extending from the Pelican and Hayden valley areas (Figure 1.2) with a maximum elevation of 2,500 meters (8,200 feet) in the east to the lower-elevation (2,000 meters [6,570 feet]) and geothermally influenced Madison headwaters area in the west (Meagher 1973; Bruggeman 2006). Winters are often severe, with temperatures reaching -42 degrees Celsius (-44 degrees Fahrenheit) and snow pack exceeding 1.8 meters (6 feet) in some areas. Bison in central Yellowstone congregate in the Hayden Valley for breeding (Meagher 1973; Geremia et al. 2011, 2014b). Afterwards, most bison move between the Madison, Firehole, Hayden, and Pelican valleys, but some travel to the northern region of the park before returning to the Hayden Valley for the subsequent breeding season (Geremia et al. 2011, 2014b; White and Wallen 2012).

Bison in northern Yellowstone primarily occupy the Yellowstone River drainage and surrounding mountains between the Lamar Valley and Mirror Plateau in the east (maximum elevation = 2,740 meters [9,000 feet]) and the lower-elevation Gardiner basin in the west (1,615 meters [5,300 feet]) (Meagher 1973; Houston 1982; Barmore 2003; Geremia et al. 2011, 2014b). The northern region of Yellowstone is drier and warmer than the rest of the park, with average snow depths ranging from about 1 meter (3.5 feet) at higher elevations to less than 0.3 meter (1 foot) at lower elevations. Bison in northern Yellowstone congregate in the Lamar Valley and on adjacent plateaus during the breeding season (Meagher 1973; Geremia et al. 2011, 2014b). More information and maps of the distribution and movements of Yellowstone bison are provided in Chapter 4.

## Feeding

Bison are ruminants with a large, multiple-chambered stomach containing microorganisms such as bacteria and protozoa that facilitate the breakdown of plant material (Van Soest 1994; Feist 2000). Grasses, sedges, and other grass-like plants comprise more than 90 percent of the diets of Yellowstone bison through the year (Meagher 1973; Singer and Norland 1994; Barmore 2003). Forbs and the leaves of woody plants comprise less than 5 percent of their diets (Meagher 1973).

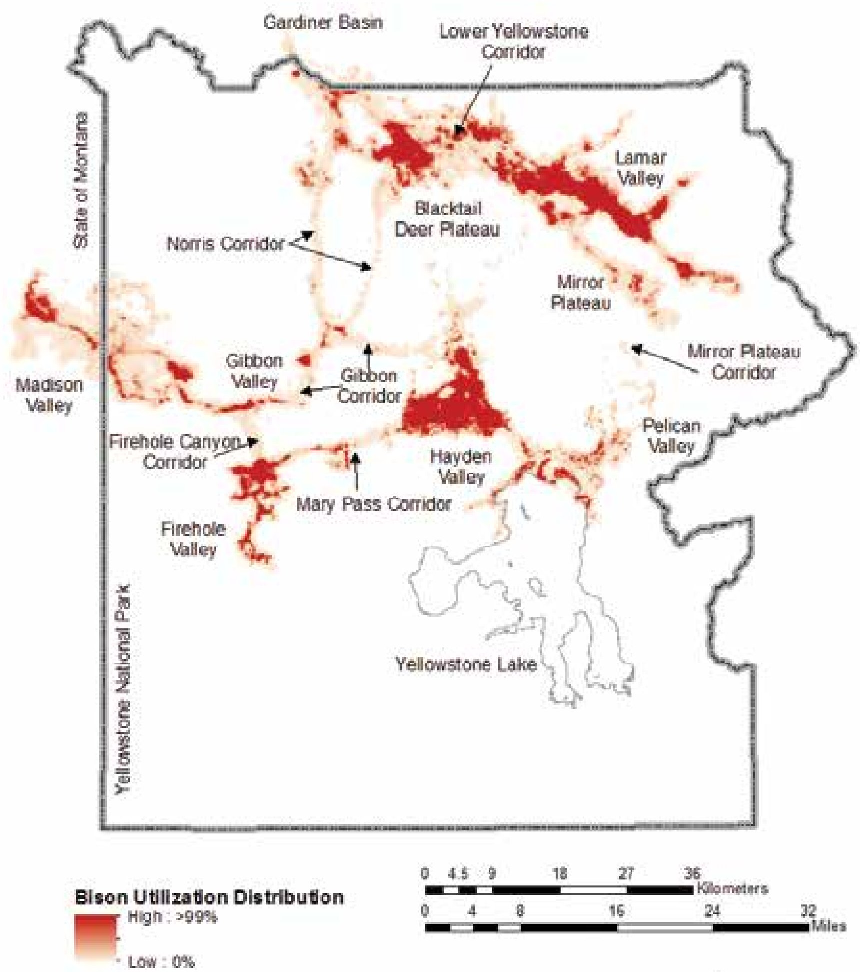


*Figure 1.2. Names of various places and areas used by bison in and near Yellowstone National Park. Darker shading indicates areas used more frequently by 66 adult female bison fit with radio collars during 2004 through 2012 (Geremia et al. 2014b).*

Yellowstone bison make foraging decisions at multiple spatial scales, including the selection of foraging areas across the landscape, foraging patches within an area, and plant species and individual plants within a foraging patch (Bruggeman 2006). The length of time bison spend foraging in an area before moving is affected by the perceived value of the area compared to other recently visited areas—including the quantity and quality of forage, amount of snow, previous foraging experiences (learning), and competition with other bison and/or other ungulates (Bruggeman 2006).

During winter, forage for bison in the Yellowstone area is mostly dead and of low quality. Thus, vegetation quality has little influence on the selection of foraging patches, and factors such as snow pack and competition that influence the availability of forage are more important (Wallace et al. 1995; Fortin et al. 2003; Bruggeman 2006). Bison tend to select foraging patches in areas with less snow because displacing snow reduces efficiency and contributes to increased energetic costs (Bjornlie and Garrott 2001). As an area becomes covered by deeper snow or occupied by numerous animals competing for forage, bison will eventually search for another area with less snow or fewer animals (Bruggeman 2006). As a result, large shifts in bison distribution may occur to lower-elevation meadows with more energy efficient foraging during severe winters (Bruggeman 2006). Furthermore, bison in central Yellowstone may choose to feed in geothermally influenced areas where the time and energetic costs of displacing snow are minimal, but the quantity of forage is relatively low and there are other costs to feeding (e.g., faster wear of teeth due to silica in the soil; high arsenic and fluoride concentrations in water and plants; Garrott et al. 2009b; Geremia et al. 2009).

During summer, bison tend to repeatedly graze productive areas, selecting grasses from dry uplands and sedges from moist sites (Wallace et al. 1995; Olenicki and Irby 2003). High densities of bison can deplete high-quality forage patches, resulting in frequent movements and substantial variation in grazing intensity across the landscape (Gates and Broberg 2011; Kohl et al. 2013). A study during summer and autumn of 1998 through 2000 found bison in the Hayden Valley foraged in upland grasslands until they had eaten 50 to 60 percent of the grasses and foraging efficiency decreased (Olenicki and Irby 2003). Bison then began moving across the valley in search of ungrazed patches or grazed patches with regrowth (Olenicki and Irby 2003). They also used moist communities adjacent to grasslands, and ate sedges and other grass-like plants after they had depleted preferred grasses in upland communities (Olenicki and Irby 2003).

Scientists in Yellowstone National Park are currently studying the effects of predators such as wolves on bison distribution, habitat selection, and foraging patterns. In Prince Albert National Park, Canada, the selection of foraging meadows by bison was primarily influenced by forage availability and quality, and secondarily by the risk of encountering wolves (Fortin and Fortin 2009; Fortin et al. 2009; Harvey and Fortin 2013). Bison were more vulnerable to predation during winter, and as a result, groups avoided areas with deep snow and ate less at each site when risk was greater (Fortin and Fortin 2009; Harvey and Fortin 2013). More information on feeding by Yellowstone bison and their ecological role can be found in Chapters 6 and 7.

## Energetics and Nutritional Condition

Metabolic rates for plains bison are about 0.12 to 0.16 megajoules per kilogram of body mass per day in winter and about 0.21 to 0.24 megajoules per kilogram per day in summer (Christopherson et al. 1979; Feist 2000). Bison reduce their metabolic rates during winter via hormonal changes in response to shorter daylight periods and colder temperatures (Christopherson et al. 1979; Feist 2000). Thus, there is a reduction in energy costs and forage intake during the time of year when prolonged under-nutrition lowers body condition (Feist 2000). Digestible energy intake for adult female bison in Yellowstone during winter ranged from 115 to 155 kilocalories per kilogram$^{0.75}$ of body mass per day, and was greater in northern than central Yellowstone (DelGiudice et al. 2001). Within central Yellowstone, intake of metabolizable energy by bison during winter was lower for bison in the Hayden Valley with deep snows


*Bison in a thermally influenced area near Obsidian Creek in the northern region of Yellowstone National Park during winter.*

than for bison in the Madison headwaters area where geothermally warmed basins reduced snow accumulation and afforded easier access to vegetation (Bruggeman et al. 2009c).

Bison gain weight during the spring and summer and lose weight during autumn and winter (Feist 2000). Yellowstone bison experience progressive nutritional deprivation, low dietary intake of minerals (e.g., sodium, phosphorus), and increased break-down of muscle mass for energy during winter (DelGiudice et al. 1994). Bison calves typically have 40 to 50 percent lower fat reserves and higher winter mortality rates than adults, especially during severe winters (DelGiudice et al. 2001). Under-nutrition and protein metabolism are usually higher in bison spending winter in central Yellowstone than for bison in northern Yellowstone (DelGiudice et al. 1994). Fat contents for adult female bison in March during the moderate winter of 1988 were 3 to 4 percent in central Yellowstone and 5 to 7 percent in northern Yellowstone (DelGiudice et al. 2001). The milder nutritional restriction of bison in northern Yellowstone is likely due to shallower snow cover and greater access to forage compared to the more severe winter conditions in central Yellowstone that limit access to forage, increase the energetic costs of foraging and movements, and in turn, lead to increased depletion of body fat and protein (Parker et al. 1984; Torbit et al. 1985; DelGiudice et al. 2001). More information on the nutritional ecology of Yellowstone bison can be found in Chapter 6.

During winter, bison in Yellowstone can either travel through unbroken snow, through broken snow on trails created by bison or other ungulates, or on roads that are either plowed for wheeled vehicles or mechanically groomed (i.e., packed snow) for over-snow vehicles such as snowmobiles and snow coaches. Coughenour (2005) estimated that 6 percent of winter travel by bison was through unbroken snow, 74 percent was through broken snow, and 20 percent was on plowed or groomed roads. Travel costs were 11 to 14 percent of total energy costs for bison in the central and northern regions of the park. Though bison readily travel through unbroken snow, they learn to sometimes move along paths of least resistance like plowed or groomed roads

(Coughenour 2005). However, 80 percent of their travel occurs off road (Bjornlie and Garrott 2001; Bruggeman et al. 2009a,b).

## Diseases

Several diseases and parasites have been detected in Yellowstone bison, including lungworms (*Dictyocaulus* sp.), tapeworms (*Moniezia benedeni*), biting flies, and several outbreaks of hemorrhagic septicemia between 1911 and 1922 that killed 9 to 15 percent of the bison in northern Yellowstone (Meagher 1973; Franke 2005; Plumb and Sucec 2006). Also, outbreaks of the deadly disease anthrax, which is caused by the bacterium *Bacillus anthracis* and transmitted by inhalation or ingestion of endospores that are found in the soil or carcasses, have occurred in domestic bison herds in the Greater Yellowstone Area (Aune et al. 2010; Adams and Dood 2011). However, these diseases and parasites have had little effect on the abundance, demography, or distribution of Yellowstone bison. Conversely, the chronic exposure of Yellowstone bison to the nonnative disease brucellosis, which is caused by the bacterium *Brucella abortus*, and can be transmitted to cattle and humans, has become a primary factor influencing bison survival (due to the culling of exposed animals) and reproduction (due to decreased birthing rates; Geremia et al. 2009; Rhyan et al. 2009). When cattle are infected, there is economic loss to producers from killing infected animals, increased disease testing requirements, and possibly, decreased marketability of their cattle. Thus, brucellosis hinders the recovery of Yellowstone bison outside the park (Lott 2002; Franke 2005; Plumb et al. 2009; Bailey 2013). More information on brucellosis and its management implications for Yellowstone bison is provided in Chapter 2.

## Population Dynamics

Historically, Yellowstone bison spent summer in the Absaroka Range north of Yellowstone National Park; in the Lamar Valley-Mirror Plateau area of northeastern Yellowstone; in the Hayden Valley of central Yellowstone; and in the Madison-Pitchstone plateaus of southwestern Yellowstone (Meagher 1973). Bison in northern Yellowstone spent

NPS/Jim Peaco

winter in the Lamar Valley and nearby areas; bison in central Yellowstone spent winter in the Hayden and Pelican valleys; and bison in southwest Yellowstone spent winter on the Snake River plains (Meagher 1973). However, bison were almost extirpated before 1900, leaving a remnant, indigenous herd of approximately 23 bison in the Pelican Valley of central Yellowstone (Meagher 1973). In 1902, managers created another herd in northern Yellowstone from 18 female bison that were relocated from a ranch in northern Montana and 3 males from Texas (Cahalane 1944; Meagher 1973). Protection and supplemental feeding enabled the bison in northern Yellowstone to proliferate to about 1,000 animals by 1928 (Meagher 1973; Fuller et al. 2007a). Likewise, the relocation of 71 animals from northern Yellowstone to central Yellowstone during 1936, combined with protection from poaching, led to an increase in the number of bison in central Yellowstone to about 1,300 by 1954 (Meagher 1973; Fuller et al. 2007a).

Frequent culling by park managers reduced bison numbers through 1966, but abundance increased rapidly after a moratorium on culling was instituted (Meagher 1973; Figure 1.3). Bison numbers increased from about 500 in 1970 to 2,000 in 1980, and 3,000 in 1990. At the same time, elk (*Cervus elaphus*) numbers in northern Yellowstone increased from about 4,000 in 1968 to 12,000 by the mid-1970s and 19,000 by 1988 (Eberhardt et al. 2007). As herbivore numbers increase in an area, the amount of forage available for each individual decreases, which can eventually reduce foraging efficiency, lead to a decrease in nutrition and body condition, and in turn, lower pregnancy and survival rates (Caughley 1976; Eberhardt 2002). As bison and elk numbers increased, however, they began to change their movement patterns and expand their winter ranges to access more food resources and avoid lower foraging efficiency (Meagher 1989b; Lemke et al. 1998; Fuller et al. 2007a; White et al. 2013b). Only a few bull bison left Yellowstone National Park before 1975, but thereafter, larger groups with female bison began migrating into Montana during winter (Meagher 1989b; Geremia et al. 2011). Also, in the 1980s bison from central Yellowstone began moving to northern Yellowstone during winter, where some of them stayed

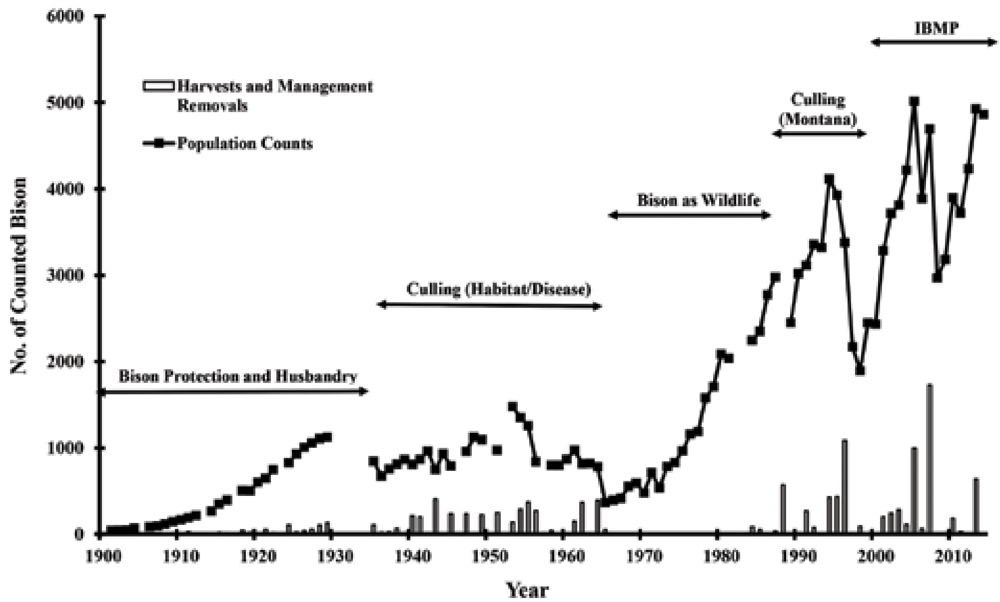


*Figure 1.3. Counts and removals of bison in Yellowstone National Park and nearby areas of Montana during 1901 through 2014. IBMP refers to the Interagency Bison Management Plan.*

and remained year-round (Fuller et al. 2007a; Bruggeman et al. 2009c). These movements were induced by high bison densities combined with deep snow packs that limited food availability during some winters in the central region of the park (Fuller et al. 2007a; Bruggeman et al. 2009c; Gates and Broberg 2011; Geremia et al. 2011).

Between 1984 and 2000, more than 3,000 bison that migrated outside Yellowstone National Park and into Montana were harvested by hunters or culled from the population to prevent the possible transmission of brucellosis from bison to cattle (White et al. 2011). In 2000, the State of Montana and the federal government agreed to an Interagency Bison Management Plan that prescribed collaborative actions to reduce the risk of brucellosis transmission from Yellowstone bison to cattle, including the culling of some bison near the park boundary, while conserving a wild population of bison with some migration to winter ranges on public lands in the state (USDI, NPS and U.S. Department of Agriculture [USDA], Forest Service [USFS], Animal and Plant Health Inspection Service [APHIS] 2000a,b).


*Bison moving along the road near Corwin Springs, Montana.*

Under this plan, counts of bison in central Yellowstone increased from 1,900 in 2000 to 3,500 in 2005 due to high reproduction, survival, and recruitment rates. Counts then decreased to 1,400 bison by 2013, primarily due to large culls of about 1,000 bison at the park boundary during winter 2005-2006 and 1,560 bison during winter 2007-2008 (Geremia et al. 2014a). Conversely, counts of bison in northern Yellowstone increased from about 500 in 2000 to 3,400 in 2014 (Geremia et al. 2014a). This rapid increase was enhanced by immigration of bison from central Yellowstone, and possibly, reduced competition as counts of northern Yellowstone elk decreased from about 19,000 in 1994 to 4,000 in 2013 following the recovery of grizzly bears (*Ursus arctos*), mountain lions (*Puma concolor*), and wolves (Smith et al. 2003; Ruth 2004; White et al. 2012; Frank et al. 2013; White and Gunther 2013). More information on the population dynamics and management of Yellowstone bison can be found in Chapter 3.

## Conclusions

The lack of tolerance for wild bison in most areas outside Yellowstone National Park is the primary factor limiting their restoration in the Greater Yellowstone Area. Large portions of the historical winter ranges used by these bison are no longer available due to agricultural, residential, and recreational development (Gude et al. 2006, 2007; Schwartz et al. 2012; White et al. 2013b). Also, there are political and social concerns about allowing bison outside the park, including human safety and property damage, competition with livestock and other ungulates for grass, diseases such as brucellosis that can be transmitted between bison and cattle, depredation of agricultural crops, and a shortage of funds for state management (Lott 2002; Boyd 2003; Franke 2005; Bailey 2013). Fortunately, many of these constraints can be remedied through the collaborative actions of federal and state agencies across jurisdictional boundaries, and the future choices of people in Montana and elsewhere (Franke 2005; Plumb et al. 2009; Bailey 2013; Becker et al. 2013). The current management of Yellowstone bison, and recommendations for the future, are discussed in Chapters 10 and 11.


NPS/Jim Peaco

*Preparing blood samples for brucellosis testing procedures.*

# Chapter 2

## BRUCELLOSIS—A NONNATIVE DISEASE HINDERING THE RESTORATION OF YELLOWSTONE BISON

*P.J. White, David E. Hallac, Rick L. Wallen, and Jesse R. White*

Wild bison and elk in the Greater Yellowstone Area were infected with *Brucella abortus* bacteria by domestic European cattle before the 1930s (Meagher and Meyer 1994). This disease decreases the birthing rates of Yellowstone bison and has indirectly influenced survival rates due to the culling of exposed animals by humans (Geremia et al. 2009; Rhyan et al. 2009). Moreover, this disease has been an overriding factor influencing the distribution and management of Yellowstone bison due to concerns about transmission of the bacteria back to cattle and economic losses to producers (USDA, APHIS 2010). Thus, brucellosis directly limits the potential for further recovery of bison in the Greater Yellowstone Area (Lott 2002; Franke 2005; Plumb et al. 2009; Bailey 2013). In contrast, elk in the Greater Yellowstone Area are managed and treated much differently, even though brucellosis is also endemic in their populations and has been repeatedly transmitted to cattle over the last decade. Because brucellosis is mentioned throughout this book, and elk are an important factor when discussing feasible brucellosis containment and suppression strategies, in this chapter we provide information about the disease, discuss attempts to suppress it in wildlife, outline the challenges of reducing transmission risk from wildlife, and recommend a pathway forward.[3]

## Bovine Brucellosis

Brucellosis is primarily transmitted within and among bison, elk, and cattle during parturition when susceptible animals ingest *Brucella* bacteria from birthing materials (amniotic fluids, fetus, placenta) or the newborn calf (Thorne et al. 1978; Williams et al. 1997; Cheville et al. 1998; Rhyan et al. 2001; Thorne 2001). A secondary mode of transmission is through milk when actively infected females nurse their calves (Rhyan et al. 2009). Females are often infected with *Brucella* bacteria at a young age, but do not shed the bacteria until they become reproductively active at approximately 3 years (Roffe et al. 1999; Rhyan et al. 2009; Treanor et al. 2011). Male bison can shed *Brucella* bacteria in semen, but do not infect females during breeding due to low numbers of bacteria present and death of those bacteria in the vagina (Robison 1994; Frey et al. 2013; Uhrig et al. 2013).

*Brucella* bacteria establish persistent infections by remaining inactive in the lymphoid system tissues of females until conditions become favorable for bacteria to multiply and spread in the reproductive tract during the latter part of gestation (Nicoletti and Gilsdorf 1997; Grovel and Moreno 2002). At that time, the bacteria can rapidly increase in cells of the placenta and induce abortions, still births, and premature live births in some animals (Rhyan et al. 1994; Nicoletti and Gilsdorf 1997; Grovel and Moreno 2002). Some females appear to recover and clear the bacteria from their bodies after this infective phase, but others retain *Brucella* bacteria and can become infective during subsequent pregnancies (Rhyan et al. 2009; Treanor et al. 2011). Also, some females

3 Portions of this chapter were included in and/or adapted from USDI, NPS (2014).

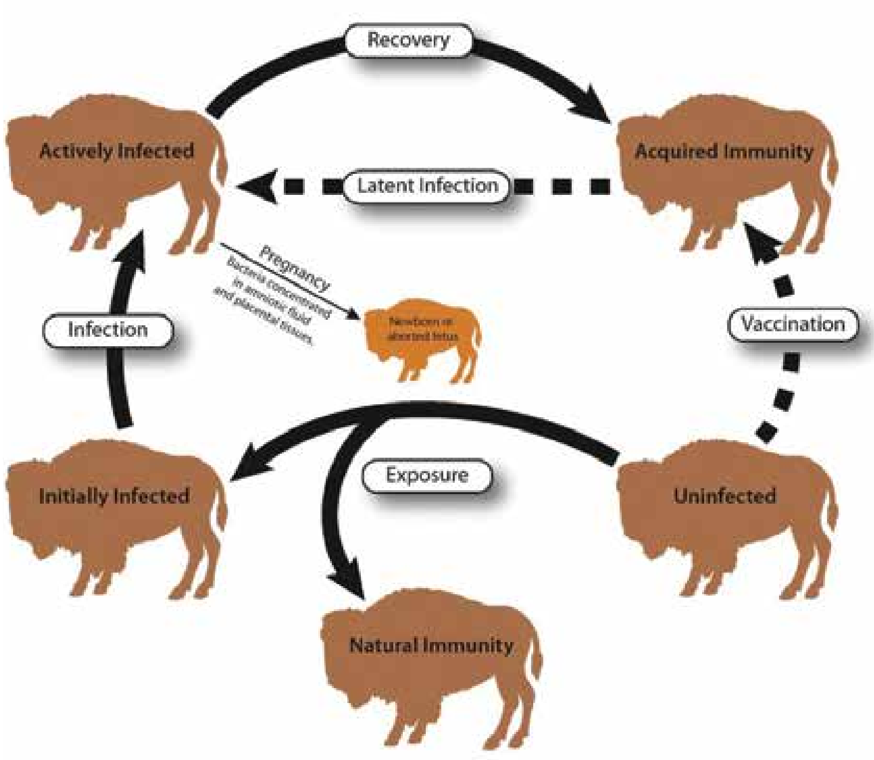


*Figure 2.1. The bovine brucellosis transmission cycle (USDI, NPS 2014).*

could be re-infected at a later time by ingesting *Brucella* bacteria from birthing materials shed by highly infected animals. However, the probability of aborting their fetus should be reduced because their immune systems should be able to recognize *Brucella* bacteria due to the previous infection (Treanor et al. 2011; Figure 2.1).

The spread of brucellosis is influenced by a variety of factors, including the proportions of females in various populations that are infectious, the amounts of bacteria encountered by susceptible individuals, and the susceptibility of animals to infection (Dobson and Meagher 1996; Williams et al. 1997; Cheville et al. 1998; Thorne 2001; Hobbs et al. 2014). Persistent, intracellular pathogens such as *Brucella abortus* are difficult for animals to clear from their immune systems, and as a result, infections may recur during periods when immune defenses are weakened (Treanor 2013). Wild bison and elk in the Greater Yellowstone Area experience chronic undernutrition and poorer body condition during winter, which reduces their immune defenses and increases their vulnerability to *Brucella* bacteria (Treanor 2013). Also, females are more susceptible to infection during pregnancies because cell-mediated immune responses against *Brucella abortus* are suppressed to safeguard developing fetuses (Treanor 2013).

For bison or elk to transmit brucellosis to cattle, they must be in the same locale and undergo an abortion or birthing event that deposits bacteria-laden tissues that are then contacted by cattle (Cross et al. 2007; Kilpatrick et al. 2009; Schumaker et al. 2010; Kauffman et al. 2013). Therefore, the risk of brucellosis transmission from wildlife to cattle also depends on: (1) forage availability and winter severity that influence the magnitude and extent of wildlife movements to low-elevation areas occupied by cattle during winter and spring, (2) the number of interactions between cattle and wildlife living in close proximity, and (3) the persistence of infectious material deposited on the landscape (Kilpatrick et al. 2009; Schumaker et al. 2010; Schumaker 2013; Hobbs et al. 2014).

## Diagnostics

To diagnose brucellosis infection with a high level of certainty, it is necessary to kill animals and attempt to culture *Brucella* bacteria from milk, lymphatic tissues, uterine discharges, and fetal tissues (Cheville et al. 1998; Thorne 2001; Roberto and Newby 2007). Culturing the bacteria depends on sampling tissues where bacteria are residing in the animal, which is not uniform and varies over time (Treanor et al. 2011). As a result, a positive culture of *Brucella* bacteria from tissue or blood definitely indicates infection, but a negative culture test does not prove the animal is not infected (Rhyan et al. 2009).

Serology is often used instead of killing animals to detect antibodies circulating in the blood that indicate past exposure to *Brucella abortus* bacteria. A positive serology test (i.e., seropositive) does not necessarily mean that the animal is still infected or capable of transmitting the bacteria, but levels of antibodies tend to be higher in animals with active infections (Rhyan et al. 2009; Treanor et al. 2011). Thus, assays such as fluorescent polarization can be used to estimate antibody levels and identify animals that are likely infectious (Treanor et al. 2011). This assay is most reliable at identifying actively infected bison older than 5 years of age, but most bison less than 3 years old that test positive for *Brucella* antibodies are actively infected with live bacteria in their tissues (Treanor et al. 2011).

### Brucellosis Prevalence, Transmission Risk, and Regulation

More than $3.5 billion have been spent since 1934 to eradicate brucellosis from cattle in the United States, with the disease being detected in less than 0.0001 percent of herds nation-wide (Cheville et al. 1998; USDA, APHIS 2009; U.S. Animal Health Association 2012; Rhyan et al. 2013b). In North America, bovine brucellosis currently persists only in bison and elk populations in the Greater Yellowstone Area and Wood Buffalo National Park in Alberta and the northwest Territories of Canada; though it is widespread world-wide and endemic in many areas of the Russian Federation and nearby countries (Cross et al. 2007; Ivanov et al. 2011; Godfroid et al. 2013; Rhyan 2013). Also, several other species of *Brucella* bacteria are endemic in certain areas of the world, including *Brucella melitensis* and *Brucella ovis* in sheep and goats, *Brucella canis* in dogs, and *Brucella suis* in swine—including feral pigs in the United States (Godfroid et al. 2013; Rhyan 2013). Cattle in Wyoming, Montana, and Idaho were declared free of brucellosis during 1983, 1985, and 1991, respectively, but bovine brucellosis was detected in more than 20 cattle or domestic bison herds in these three states during 2002 to 2013 (U.S. Animal Health Association 2012; Rhyan et al. 2013b). These transmissions were traced to wild elk using epidemiology or genetic tests, and apparently occurred due to increases in brucellosis prevalence in elk and contacts between elk and cattle on shared winter ranges (Beja-Pereira et al. 2009; U.S. Animal Health Association 2012; Cross et al. 2013). To date, no cases of brucellosis transmission from wild bison to cattle have been detected, though such transmission is possible and risk increases as winter severity and the number of bison migrating into areas with cattle increase (Kilpatrick et al. 2009; Schumaker et al. 2010; Rhyan et al. 2013b; Schumaker 2013).

Approximately 5,700 wild bison occur in two populations (Jackson, Yellowstone) in the Greater Yellowstone Area, and these bison move across about 1.2 million acres (485,620 hectares) of mostly public lands. The prevalence of brucellosis in Yellowstone bison is relatively high with about 60 percent of adult females testing seropositive for antibodies in their blood indicating previous exposure to *Brucella* bacteria (Hobbs et al. 2014). However, only about 10 to 15 percent of all adult female bison, and 20 to 30 percent of seropositive female bison, are infectious and could potentially shed live bacteria (Roffe et al. 1999; Rhyan et al. 2009; Hobbs et al. 2014). Also, the risk of brucellosis transmission from bison to cattle is negligible because: (1) management successfully limits bison movements and mingling with cattle, (2) bison calving mostly occurs in April and May before cattle are released on summer ranges, and (3) bison naturally move to higher elevation summer ranges in national parks following snow melt and vegetation green-up (Kilpatrick et al. 2009; Schumaker et al. 2010; White et al. 2011; Rhyan et al. 2013b; Schumaker 2013).

Approximately 30,000 to 40,000 elk live in the Greater Yellowstone Area in numerous populations (Schumaker et al. 2012). As many as 18,000 of these elk may be supplementally fed during winter at the National Elk Refuge and 22 state-operated feeding grounds in northwestern Wyoming (Scurlock et al. 2010a; Schumaker 2013). Elk aggregate at these feeding grounds in the southern portion of the Greater Yellowstone Area because there is insufficient low-elevation habitat to support current numbers due to human encroachment on their historic winter range (Smith et al. 2004). Late winter coincides with late gestation and the time when elk are likely to transmit *Brucella* bacteria via abortion events (Cross et al. 2007, 2010). Thus, the prevalence of brucellosis in elk at these feeding grounds was historically quite high (10 to 35 percent) compared to other elk populations (0 to 6 percent) in the Greater Yellowstone Area (Barber-Meyer et al.


*Bison and elk in the Lamar Valley of Yellowstone National Park.*

2007; Cross et al. 2007, 2010; Maichak et al. 2009; Proffitt et al. 2010a; Scurlock and Edwards 2010).

Many disease regulators believed brucellosis would not persist in elk throughout the Greater Yellowstone Area without frequent transmission from wild bison or elk dispersing from winter feeding grounds (Rhyan et al. 2013b; Schumaker 2013). However, surveillance during the past decade indicates brucellosis prevalence has increased from less than 5 percent to 8 to 25 percent in several elk populations in the northern portion of the Greater Yellowstone Area (Cross et al. 2010). These increases coincided with increasing elk numbers and/or aggregations of elk on lower-elevation winter ranges, including a greater proportion of private land than 20 years ago (Cross et al. 2010; Proffitt et al. 2010b, 2013). Many of these elk populations appear to support the disease independently of wild bison or feed-ground elk (Cross et al. 2010; U.S. Animal Health Association 2012; Rhyan et al. 2013b). Also, in recent years the distribution of elk testing positive for brucellosis exposure has expanded beyond the periphery of the Greater Yellowstone Area and now encompasses more than 20 million acres (8 million hectares).

*Total eradication of brucellosis as a goal is more a statement of principle than a workable program at present; neither sufficient information nor technical capability is available to implement a brucellosis-eradication program in the Greater Yellowstone Area.*

The estimated risk of brucellosis exposure to cattle from Yellowstone bison is insignificant (less than 1 percent) compared to elk (more than 99 percent of total risk) because elk have a larger overlap with cattle and are more tolerated by managers and livestock producers (Schumaker et al. 2010). Many of the approximately 450,000 cattle in the Greater Yellowstone Area are fed on private land holdings during winter and released on public grazing allotments during summer—but throughout the year they are allowed to mingle with wild elk (Schumaker et al. 2012; Schumaker 2013). Thus, the risks of brucellosis transmission to cattle are primarily from wild elk, and management to suppress brucellosis in bison will not substantially reduce the far greater transmission risk from elk (Kilpatrick et al. 2009; Schumaker et al. 2010; Rhyan et al. 2013b; Schumaker 2013). Therefore, numerous independent evaluations have recommended that management actions for brucellosis focus on maintaining separation between bison and cattle, while attempting to decrease elk density and group sizes in areas where mingling with cattle occurs (Keiter 1997; Cheville et al. 1998; Schumaker et al. 2010; Cross et al. 2013; Godfroid et al. 2013; Treanor et al. 2013).

To reduce the economic loss to producers when cattle are sporadically infected with brucellosis, the Animal and Plant Health Inspection Service changed their regulations in 2010 to allow livestock producers to eliminate outbreaks of brucellosis in cattle on a case-by-case basis, without imposing corrective regulations on the rest of the producers in the state. Historically, the Animal and Plant Health Inspection Service reclassified an entire state or area if two or more herds were found to have brucellosis within a 2-year period or if a single brucellosis-affected herd was not depopulated within 60 days (USDA, APHIS 2010). This reclassification often had adverse economic consequences on producers state-wide because a "brucellosis-free" classification allowed them to export cattle to other states or nations without testing (Bidwell 2010). Today, the entire state is not reclassified or subject to corrective actions provided that outbreaks are investigated and contained by removing all cattle testing positive for brucellosis exposure (USDA, APHIS 2010). In fact, brucellosis was detected in several domestic bison and cattle herds in Idaho, Montana, and Wyoming during 2009 through 2014, without any state-wide corrective actions being implemented (U.S. Animal Health Association 2012; Brown 2013).

These regulatory changes by the Animal and Plant Health Inspection Service focused increased attention on the Greater Yellowstone Area where brucellosis is chronic in bison and elk. As a result, livestock regulatory agencies in Idaho, Montana, and Wyoming defined designated surveillance areas where elk testing positive for brucellosis exposure are known or thought to exist and could mingle with livestock and expose them to tissues containing *Brucella* bacteria (Barton 2013; Logan and Correll 2013; Zaluski 2013). The combined designated surveillance areas cover approximately 71,290 square kilometers (27,525 square miles) in eastern Idaho, southwest Montana, and western Wyoming (Figure 2.2). Within these areas there are requirements for


*Figure 2.2. The Designated Surveillance Area (gold color) for brucellosis in eastern Idaho, southwest Montana, and western Wyoming. Abbreviations: DSA = Designated Surveillance Area; GYA = Greater Yellowstone Area.*

calfhood vaccination for brucellosis and individual identification for all cattle to enable traceability. Also, all sexually intact cattle must be tested for brucellosis exposure prior to sale or movement out of the designated surveillance areas. This testing provides assurance to trading partners and other state veterinarians that brucellosis-infected livestock will not be moved into their states (Barton 2013; Logan and Correll 2013; Zaluski 2013). These designations also benefit producers by eliminating unnecessary testing elsewhere and providing for the reimbursement of testing costs. The Montana Department of Livestock (MDOL 2013) estimated that the designated surveillance area provided a net annual benefit of at least $5.5 million to producers.

## Attempts to Suppress Brucellosis

Population Reduction—There have been several attempts to suppress the prevalence of brucellosis in wild bison and elk in the Greater Yellowstone Area. Managers at Yellowstone National Park periodically removed some bison and elk during 1908 to 1967 to reduce numbers and the prevalence of brucellosis (Barmore 1968). About 810 bison were relocated to other areas and 4,200 bison were shipped to meat processing facilities (Skinner and Alcorn 1942; Meagher 1973). Also, about 13,500 elk were relocated, 13,000 elk were shot or trapped in the park, and 45,000 elk were harvested by hunters north of the park (Houston 1982). Fewer than 500 bison and 4,000 elk were counted by 1968, and at that point, park managers concluded they would only eradicate brucellosis by eliminating bison and elk—which was counter to their mission of conserving these resources unharmed for the benefit and enjoyment of people (Barmore 1968; Meagher 1973; Houston 1982). Thus, culling ceased and wildlife numbers were allowed to fluctuate in response to predators, resource limitations, weather, and hunting outside the park (Houston 1982; National Research Council 2002; White and Gunther 2013).

Test-and-Slaughter — The Wyoming Game and Fish Department spent $1.3 million on a 5-year effort at several feeding grounds to capture 2,624 elk, test 1,286 female elk, and cull 197 animals testing positive for brucellosis exposure (Scurlock et al. 2010; Schumaker et al. 2012). Brucellosis prevalence was reduced from approximately 37 to 5 percent, but the extent to which this reduced the risk of transmission to cattle was unknown (Schumaker et al. 2012). Prevalence will likely increase after the cessation of suppression efforts, and economic costs make it infeasible to use this approach across the entire Greater Yellowstone Area (Schumaker et al. 2012). Test-and-slaughter programs that only remove modest numbers of elk (10 to 25 percent) are unlikely to control brucellosis across the Greater Yellowstone Area, and could facilitate transmission somewhat by removing animals that have recovered from previous infection and may have some resistance to future exposure (Bienen and Tabor 2006).

In addition, about 3,580 Yellowstone bison have been captured and shipped to meat processing or research facilities since 2000 to reduce numbers and brucellosis prevalence (White et al. 2011). These culls were extremely controversial and did not decrease brucellosis prevalence (White et al. 2011). As a result, bison managers decided to minimize the future shipment of large numbers of bison to meat processing facilities and use other tools such as conservation easements, hunting, and increased tolerance on public lands to limit bison numbers and lessen conflicts with cattle and humans (USDI, NPS et al. 2008).

Dispersed Feeding—Brucellosis transmission is strongly influenced by the density of bison or elk in close proximity during February through June when most brucellosis-induced abortions occur (Cross et al. 2013). As a result, management actions that prevent large aggregations of wildlife on winter ranges could decrease transmission. The Wyoming Game and Fish Department is trying to reduce large aggregations of elk on several feeding grounds by distributing food across a broader area and stopping feeding earlier in the year (Cross et al. 2013). However, early movements of elk away from feeding grounds could actually increase contacts between elk and nearby cattle (Cross et al. 2013).

Hunting—Targeted hunts during late winter could be used to disperse large groups of bison or elk, move them away from cattle, and/

or reduce population sizes (Cross et al. 2013). Targeted hunts for elk have been implemented in some areas of southwestern Montana and western Wyoming in recent winters, but it is too soon to evaluate their effects on brucellosis transmission (Cross et al. 2013). Also, there are many landowners in the Greater Yellowstone Area that do not allow hunters access to their lands. Elk have learned to use these areas, which can result in large aggregations during winter that could facilitate brucellosis transmission (White et al. 2012; Proffitt et al. 2013).

Bison hunting in Montana occurs outside the northern and western boundary areas of Yellowstone National Park, with harvests varying from year-to-year depending on how many bison move outside the park in response to snow depths in the higher mountains (Geremia et al. 2011, 2014b; White et al. 2011). To date, hunting has not reduced the prevalence of brucellosis in the population because infectious animals are not selectively shot. Also, many hunters select bulls, which do not transmit the disease. In addition, bison reactions to hunting pressure include moving back into the park and/or remaining inside the park where hunting is prohibited.

Predators and Scavengers—The transmission of brucellosis could be reduced by protecting predators and scavengers that reduce densities of bison and elk and quickly remove infectious birthing materials from the environment (Cross et al. 2013). Numbers of elk that spend winter and spring in Yellowstone National Park and nearby areas have decreased by about 70 percent due, in part, to predation by wolves and other large carnivores (Barber-Meyer et al. 2008; Hamlin et al. 2009; White and Garrott 2013). This reduction may have decreased the risk of brucellosis transmission to cattle due to fewer infectious elk, fewer elk aggregations, and smaller group sizes in some areas (Barber-Meyer et al. 2007; Cross et al. 2010; White et al. 2012). Also, the recovery of wolves and grizzly bears in the Greater Yellowstone Area has increased the amount of carrion, and in turn, the abundance of scavengers that could remove *Brucella*-infected tissues before they are discovered by susceptible bison, cattle, or elk (Garrott et al. 2013). The Wyoming Game and Fish Department protects scavengers such


*Infrared image of a grizzly bear on an elk carcass in Yellowstone National Park.*

as coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) on some elk feedgrounds to reduce the time infectious tissues remain on the landscape (Cross et al. 2013).

Vaccination—Three vaccines that consist of live, weakened strains of *Brucella abortus* bacteria are used world-wide to provide bison, cattle, elk, and other domestic and wild ungulates with some resistance to brucellosis infection and abortions (Olsen 2013). Elk on feeding grounds in Wyoming have been vaccinated with strain 19 vaccine since 1985. However, the *Brucella* infection rate in vaccinated and unvaccinated elk is similar, and 75 percent of vaccinated elk aborted their fetus when they were subsequently exposed to *Brucella* bacteria (Cross et al. 2013). Likewise, several experimental studies with elk detected little protection against brucellosis infection or abortion after vaccination with strain 19 (Kreeger et al. 2000, 2002; Olsen 2013). Some elk developed antibody responses after vaccination, but they did not develop the cellular immune responses needed to suppress *Brucella* bacteria inside cells (Olsen and Johnson 2012; Olsen 2013). Similarly, vaccination with strain 19 did not protect bison calves from subsequent infection and abortions (Davis et al. 1990, 1991; Olsen 2013). Two-thirds of vaccinated bison aborted their pregnancies, though vaccinated animals did have fewer abortions and lower infection rates thereafter (Davis et al. 1991).

Serological tests for *Brucella* antibodies cannot distinguish between an animal that has been infected with field strains of the bacteria and those which have been vaccinated with strain 19 (Cheville et al. 1998). Consequently, many infections identified in livestock populations were thought to be vaccine related. Strain 19 vaccine was replaced with strain RB51 vaccine, which causes animals to produce antibodies that do not react on standard brucellosis serological tests. Cattle operations in the designated surveillance areas of Idaho, Montana, and Wyoming vaccinate all calves and most adults with strain RB51 vaccine, which reduces abortions and further transmissions from cattle that subsequently become exposed to, and infected with, *Brucella* bacteria (Olsen et al. 1998, 2009). However, the vaccine does not prevent cattle from becoming infected after exposure to infectious amounts of *Brucella* (Olsen and Tatum 2010). Thus, vaccinating cattle with strain RB51 will not eliminate the potential for brucellosis infection from wildlife (Olsen 2013).

Similarly, strain RB51 vaccine does not prevent bison or elk from becoming infected following exposure to sufficient doses of *Brucella* bacteria (Treanor et al. 2010; Olsen 2013). In experiments, less than 15 percent of bison vaccinated with strain RB51 were protected against infection following exposure to *Brucella* bacteria (Elzer et al. 1998; Davis and Elzer 1999, 2002; Olsen et al. 2003). Also, vaccinated elk had little protection against brucellosis infection or abortion (Kreeger et al. 2000, 2002; Olsen 2013). In captive settings, strain RB51 vaccine reduces abortions and further transmissions of brucellosis in about 50 to 60 percent of bison, especially when they receive a subsequent booster vaccination (Olsen et al. 1998, 2009; Plumb and Barton 2008; Treanor 2012; Olsen 2013). However, Treanor (2012) found the magnitude of immune responses from single RB51 vaccinations in wild bison were more variable and often substantially lower, likely due to the poorer nutritional status of wild bison during winter. During 2004 to 2011, non-pregnant Yellowstone bison were sporadically vaccinated with strain RB51 at boundary capture facilities. However, only 299 animals were vaccinated and this low level of effort had no effect on brucellosis prevalence in the population (White et al. 2011; USDI, NPS 2014).

Strain 82 vaccine has been used to reduce outbreaks of brucellosis in cattle in some regions of the Russian Federation (Olsen et al. 2010; Ivanov et al. 2011; Denisov et al. 2013). In 1974, more than 5,300 cattle herds were infected with *Brucella abortus* across the Soviet Union. However, only 68 herds remained infected after widespread use of strain 82 vaccine for 34 years (Olsen et al. 2010; Ivanov et al. 2011). These results appear promising, but the vaccine is not approved for use in the United States and it will likely take many years to adequately test the vaccine and possibly gain approval.

Fertility Control—Model simulations suggest that inhibiting fertility in bison testing positive for brucellosis exposure could decrease future transmission (Ebinger et al. 2011). Female bison 3 to 5 years old have a higher probability than older bison of being infectious and transmitting *Brucella* bacteria during parturition (Treanor et al. 2011). Therefore, preventing young female bison and elk from breeding for several years could decrease the risk of brucellosis transmission if they were no longer infectious after returning to reproductive status (Miller et al. 2004; Rhyan et al. 2013a; USDI, NPS and Montana Fish, Wildlife & Parks [MFWP] 2013). Immunocontraceptive vaccines are currently being investigated for possible use in bison and other wildlife, including porcine zona pellucida (PZP) and gonadotropin releasing hormone (GnRH). The PZP vaccines induce the formation of antibodies that block sperm from fertilizing eggs, while GnRH vaccines prevent follicle growth and ovulation (Kirkpatrick et al. 1996; Miller et al. 2004; USDA, APHIS 2012; National Research Council 2013). In 2012, the Animal and Plant Health Inspection Service initiated a 6-year study using GnRH vaccine (GonaCon™) on captive Yellowstone bison. The objectives of the study are to determine if the vaccine prevents the shedding of *Brucella* bacteria and whether bacteria that remain dormant or latent will proliferate during pregnancies after the effects of contraception wane (USDA, APHIS 2012).

No fertility control methods that are affordable, easily delivered, highly effective, and reversible are currently available for delivery to wild bison and elk that are spread across a vast landscape. There is no contraceptive product for oral delivery that is species- and gender-specific, and remote delivery via bio-absorbable projectile or dart is not feasible for most wide-ranging wildlife populations (Garrott and Oli 2013; National Research Council 2013; USDI, NPS 2014). Also, all contraceptive methods would alter the behavior and/or physiology of wild bison or elk to some extent because, by design, they affect the animal's reproductive system (National Research Council 2013). Infertility may last longer than expected and even become permanent, especially after repeated vaccinations (National Research Council 2013). In addition, preventing births in enough females could change the age structure of a population by reducing the number of young


*Female bison and calf near the Lamar Valley in the northern region of Yellowstone National Park.*

and enhancing the survival of infertile females that no longer have energetic costs from pregnancy and lactation (National Research Council 2013). Furthermore, fertility control can contribute to artificial selection pressures that lead to unintended genetic consequences (Ransom et al. 2013). As a result, the implementation of fertility control using current knowledge and techniques could lead to long-term, unintended consequences to bison and elk populations in the Greater Yellowstone Area (White et al. 2013c; USDI, NPS 2014).

## Economic Assessments of Preventative Actions

Economists, biologists, and veterinarians in Wyoming evaluated feasible management strategies to reduce the risk of cattle herds contracting brucellosis from wild elk (Roberts et al. 2012; Kauffman et al. 2013). Cattle producers could take several actions to reduce this risk, including: (1) fencing haystacks, (2) hazing elk from their property, (3) booster vaccinating adult cattle, (4) spaying heifers, (5) modifying winter feeding schedules, (6) delaying cattle release on summer grazing allotments, and (7) preventing the mingling of cattle and wildlife (Roberts et al. 2012). However, these preventative actions are not cost-effective for most cattle producers due to the apparent randomness of brucellosis outbreaks, the high cost of prevention measures compared to their effectiveness, and the comparatively low cost of dealing with an occasional brucellosis outbreak in cattle (Roberts et al. 2012).

Researchers also compared the costs and benefits of implementing management strategies with wild elk to increase the number of years until a brucellosis outbreak occurred in cattle (Kauffman et al. 2013). The evaluated management strategies were: (1) capturing elk and removing animals testing positive for brucellosis exposure, (2) vaccinating calf elk, and (3) lower-density feeding of elk on feedgrounds to avoid large aggregations (Kauffman et al. 2013). These management strategies could increase the time between brucellosis outbreaks in cattle, but the costs would be extremely high relative to the benefits

(Kauffman et al. 2013). As a result, these preventative actions are not cost-effective to implement (Kauffman et al. 2013).

### Challenges of Reducing Brucellosis Transmission Risk

Disease regulators have recommended the use of vaccines to reduce brucellosis infection in wildlife in the Greater Yellowstone Area. However, their use is limited due to financial, logistic, scientific, and social constraints (Cross et al. 2013; Godfroid et al. 2013; Olsen 2013; White et al. 2013c). A successful vaccination program to reduce brucellosis transmission in bison and elk would require the consistent delivery of known doses of vaccine to most females in autumn. This timing would facilitate the generation of sufficient protective immune responses before potential exposure to *Brucella* bacteria during February through June (Plumb and Barton 2008; Treanor 2012). However, bison and elk inhabit millions of acres across the ecosystem and it would be difficult to capture a majority of their populations in facilities for vaccination (Cross et al. 2013; White et al. 2013c). Also, remote delivery of vaccine using darts or bio-absorbable bullets is challenging because approach and delivery of any projectile disturbs wild animals, which could preclude the delivery of vaccine to many of the individuals in larger groups (USDI, NPS 2014). In addition, it would be difficult to deliver an oral vaccine to bison and elk by attracting them to bait because they are herbivores (USDI, NPS 2010). Moreover, a vaccination program for bison and elk would need to be maintained in perpetuity to prevent resurgences in prevalence (White et al. 2013c). Capture and remote vaccination are likely unpleasant experiences for bison and elk, and therefore, they may begin to avoid humans. As a result, it will probably become more difficult to vaccinate large portions of bison and elk populations in the Greater Yellowstone Area over time (USDI, NPS and MFWP 2013; White et al. 2013c; USDI, NPS 2014). In turn, behavioral effects on bison and elk such as reduced tolerance of people and vehicles could lead to shifts in their spatial distribution across the landscape and reduce opportunities for visitors and hunters to observe bison and elk (USDI, NPS and MFWP 2013).

It may be possible to capture and/or remotely vaccinate more bison and elk when they aggregate on their winter ranges. However, vaccination often stimulates less of a protective immune response in undernourished animals (Treanor 2012, 2013). Bison and elk in the Greater Yellowstone Area are undernourished through winter due to the limited availability of relatively low quality forage (grasses and grass-like plants), most of which is senescent and covered by snow (DelGuidice et al. 1994, 2001). This seasonally poor nutrition and body condition increases the vulnerability of animals to bacterial infections and coincides with increasing energy and protein demands during late pregnancy; which in turn, limit the resources available for immune defense (Clemens et al. 1979; Weinberg 1987; Jolly and Fernandes 2000). Treanor (2012, 2013) found that brucellosis infection was higher in Yellowstone bison in below-average condition, which suggests that fewer bison successfully avoid infection with *Brucella* bacteria during severe or prolonged winters. Also, fat and protein metabolism strongly influenced the intensity of *Brucella* infections and immune responses in yearling female bison (Treanor 2012, 2013). As a result, the vaccination of wild bison or elk during winter may be less effective against brucellosis than suggested by the results of captive, experimental studies (Treanor 2012, 2013).

Given these challenges, we conclude that the eradication or substantial suppression of brucellosis in bison and elk in the Greater Yellowstone Area is not feasible at this time without attempting depopulation or capture, test-and-slaughter, and vaccination on a regional scale; which most stakeholders deem unacceptable and impossible (Bienen and Tabor 2006; MFWP 2013; Treanor et al. 2013). This infeasibility is due to:

- The absence of easily distributed and highly effective vaccines;
- Limitations of current diagnostic and vaccine delivery technologies;
- Effects of bison and elk nutrition, condition, and pregnancy/lactation that lessen protective immune responses;

- Potential adverse consequences (e.g., injuries, changes in behavior) to wildlife and visitor and hunter experiences from intrusive brucellosis suppression activities; and
- Our limited understanding of bison and elk immune responses to brucellosis suppression actions such as vaccination (Cross et al. 2013; Godfroid et al. 2013; Olsen 2013; Treanor 2013; USDI, NPS and MFWP 2013; White et al. 2013c).

This conclusion has been reached by several diverse and independent groups of citizens, regulators, and scientists that agree the vaccination of wild bison and elk with existing technologies and under current conditions will not solve the problem of occasional brucellosis transmission to cattle in the Greater Yellowstone Area. For example, the National Academy of Sciences concluded that "total eradication of brucellosis as a goal is more a statement of principle than a workable program at present; neither sufficient information nor technical capability is available to implement a brucellosis-eradication program in the Greater Yellowstone Area" (Cheville et al. 1998). Also, the Citizens Working Group on Yellowstone Bison (2011) indicated that "remote vaccination of wild bison using the current vaccine and delivery method as a means of reducing a risk of transmission should not be a priority at this time." Likewise, an expert bison/brucellosis science panel indicated that "the best available data do not support that vaccination of wild bison with currently available vaccines will be effective at suppressing brucellosis to a level that changes bison management strategies under the Interagency Bison Management Plan" (USDI, NPS and MFWP 2013). Similarly, the Elk Management Guidelines in Areas with Brucellosis Working Group for the State of Montana did not recommend vaccination of wildlife but indicated that "eradication of brucellosis in elk is ultimately desirable, but it is not currently feasible, and current methods to achieve this goal, such as test-and-slaughter, are unacceptable" (MFWP 2013). Moreover, the State Veterinarian of Montana was quoted as saying "the reason why the wildlife brucellosis issue hasn't been addressed is because there's no easy solution. We don't have a vaccine that's effective enough, and don't have a delivery mechanism that works for wildlife" (Chaney 2014).

Some modeling efforts have suggested that substantial reductions in brucellosis transmission are feasible within a few decades using vaccination and/or other activities (Treanor et al. 2010; Ebinger et al. 2011). However, these authors acknowledged their analyses were based on some simplifying assumptions (e.g., 100 percent efficacy and lifetime treatment effects) that were necessary to reduce model complexity and enable direct comparisons of differences among treatments. Also, these models were unable to make accurate, precise estimates of suppression amounts and timelines due to uncertainty in the parameters used to inform the models (e.g., weather, abundance of bison, and shifts in behavior in response to management actions). Hobbs et al. (2014) found including uncertainty in the number of bison that could be removed, hunted, or vaccinated substantially reduced the chances of meeting brucellosis suppression goals to less than 5 percent (USDI, NPS and MFWP 2013).

## Conclusions

Elk and bison in the Greater Yellowstone Area have been affected by the disease brucellosis (*Brucella abortus*) for almost a century. The disease has not had substantial deleterious effects on wildlife populations, but it presents an economic risk to cattle producers. As a result, livestock managers want more permanent solutions, including brucellosis eradication and complete elimination of risk to cattle (Bidwell 2010). The risk of brucellosis transmission from bison to cattle also devalues bison as wildlife outside national park units, limits tolerance for their migration to essential low-elevation winter ranges in surrounding states, and prevents relocations elsewhere to enhance conservation of the species (Franke 2005; White et al. 2011; Bailey 2013). Therefore, many wildlife managers would likely support the substantial suppression of brucellosis if and when it was biologically feasible, economically practicable, socially acceptable, and could be accomplished without harming the integrity of wildlife populations.

As discussed previously, however, the reality is that eradication or even a substantial reduction of brucellosis in bison and elk is not attainable at this time given available technologies (Cross et al. 2013; White et al. 2013c).

An effective brucellosis control program for wildlife in the Greater Yellowstone Area would require the de novo development of highly effective vaccines for both elk and bison, a delivery system that can cost-effectively provide the vaccine to thousands of female bison and tens of thousands of female elk across tens of millions of acres in the states of Idaho, Montana, and Wyoming. Biologists would also need new diagnostics that allow them to discriminate between previously infected and infectious animals to gauge vaccination efficacy (Bienen and Tabor 2006; Treanor et al. 2010; MFWP 2013). The development of separate vaccines for bison and elk would likely be necessary due to their different physiologies and protective immune responses (Cross et al. 2013; Godfroid et al. 2013; Olsen 2013). However, there has been little progress in vaccine development, delivery systems, and diagnostics due to a lack of market incentives and restrictions on research due to the classification of *Brucella abortus* as a select agent that could be packaged as a biological weapon by terrorists and used to threaten public health or national security (www.selectagents.gov). Thus, the current best alternative for wildlife and livestock managers is to suppress the probability of *Brucella abortus* transmission by maintaining separation between bison, elk, and cattle during the transmission period from February through June (Keiter 1997; Bienen and Tabor 2006; Nishi 2010; Cross et al. 2013; Godfroid et al. 2013; Treanor et al. 2013; White et al. 2013c).

Given the myriad problems to overcome to substantially reduce brucellosis infection in wild bison and elk distributed across a vast region, we suggest an alternate approach to protect domestic livestock: developing an infection-blocking vaccine for cattle. This alternative would have a much higher likelihood of effectively reducing brucellosis transmission risk in a shorter period of time because of the better understanding of cattle as a model in the veterinary sciences, the substantially larger number of facilities available for research on cattle, the better nutritional condition of cattle that may increase vaccination success, and the ability to efficiently capture and vaccinate all cattle. Current cattle vaccines are only 65 to 70 percent effective against abortion and 10 to 15 percent effective against infection (Olsen et al. 1998; Olsen and Tatum 2010). Thus, there is substantial room for improvement. Although significant resources have been expended to develop and test vaccines in the past, there have been several advances in recent years (e.g., DNA vaccines, nanoparticles) that suggest breakthroughs may still be possible (Olsen 2013; Yang et al. 2013). We realize the development of a perfect vaccine that prevents brucellosis infection in cattle will be challenging, but it seems logical to fully explore this prospect before embarking on the much more complex and difficult task of developing and delivering multiple vaccines for wildlife across a vast geographic scale. Brucellosis was eliminated in cattle historically due to the captive and controlled nature of managing livestock, and all of the factors that made it possible still exist. Moreover, if a highly effective vaccine was developed for cattle, it would likely be somewhat effective in bison and perhaps elk, so that wildlife practitioners could then focus on effective delivery to contain and suppress brucellosis.


*Park Ranger Ray Frazier with bison calf "Buff" at the Buffalo Corral in Mammoth Hot Springs, Yellowstone National Park, circa 1926.*

# Chapter 3

## HISTORICAL PERSPECTIVE—FROM NEAR ERADICATION TO LIVESTOCK TO WILDLIFE

*Rick L. Wallen, P.J. White, and Chris Geremia*

Though bison were nearly eradicated across the Great Plains by the late 1800s, there were at least hundreds and perhaps thousands of bison in the Greater Yellowstone Area during the 1870s and 1880s (McHugh 1972; Isenberg 2000). Around the time the park was established in 1872, an observer noted the lower Gardiner basin near the northern boundary "would be covered with bison" (Potter 1962). Also, Superintendent Philetus Norris reported in 1880 approximately 200 bison spent the summer near Crevice, Hellroaring, and Slough creeks and winter in the Lamar Valley in northern Yellowstone (Schullery and Whittlesey 1992). A second herd of about 100 bison spent summer in the high-elevation country between the Lamar Valley and the Grand Canyon of the Yellowstone River and winter in either the Pelican Valley or the Lamar Valley (Schullery and Whittlesey 1992). A third herd of about 300 bison spent summer on the Madison Plateau in west-central Yellowstone and winter outside the park to the west (Schullery and Whittlesey 1992).[4]

Yellowstone National Park was established, in part, to protect against the wanton destruction of fish and game found within the park (U.S. Code, Title 16, § 22, 17 Statute 32). A detachment of the First U.S. Cavalry was sent to the park in 1886, but poachers continued to kill bison and other wildlife because few remained elsewhere (Franke 2005; Whittlesey and Schullery 2011). It was not until Congress passed the Lacey Act in 1894 that soldiers had the authority to prosecute individuals for killing or transporting wildlife from the park (Haines 1977; Whittlesey and Schullery 2011). By then, bison in and adjacent to the northern region of Yellowstone had been extirpated, and only about 23 bison were left in the Pelican Valley of central Yellowstone by 1901 (Meagher 1973). This remnant, indigenous herd was the largest remaining wild population of plains bison south of Canada and was completely isolated from other populations (Meagher 1973; Bartlett 1985).

## Protection, Husbandry, and Ranch Management

Restoration of bison to the northern region of Yellowstone National Park began in 1902 with the reintroduction of 18 females from the Pablo-Allard herd in northwestern Montana and 3 bulls from the Goodnight herd in Texas (Cahalane 1944; Meagher 1973). Also, during 1903 to 1909 a few calves were taken from the indigenous bison remaining in central Yellowstone and released into northern Yellowstone (Cahalane 1944; Meagher 1973). The bison in northern Yellowstone were initially held in a fenced pasture near Mammoth Hot Springs, and then moved to the "Buffalo Ranch" in the Lamar Valley during 1907 (Meagher 1973). These bison were herded during the day and put in a fenced pasture at night, with little effort to recreate a wild population (Meagher 1973). Sometime between 1915 and 1920, the bison were allowed to roam more freely and at higher elevations during summer, while the National Park Service produced hay in the valley

4 Portions of this chapter were adapted from White et al. (2011).


*Bison at the Buffalo Ranch in the Lamar Valley of Yellowstone National Park, circa 1930.*

bottom (Meagher 1973). During this time, the reintroduced bison from northern Yellowstone probably began to mingle with the remaining indigenous bison from central Yellowstone on the Mirror Plateau and in the upper Lamar Valley towards the eastern boundary of the park (Meagher 1973, 1989b; Meagher et al. 2002; Plumb and Sucec 2006). After 1921, a deliberate effort was made to keep bison from northern Yellowstone on these higher elevation summer ranges by fencing the hay fields in the valley (Meagher 1973). Mingling with the wild bison from central Yellowstone likely increased during summer, but bison from northern Yellowstone were still rounded up in late autumn, corralled, and fed hay at the Buffalo Ranch during winter (Cahalane 1944; Meagher 1973). Bison numbers in northern Yellowstone increased rapidly under this protection and husbandry, reaching about 1,100 by 1930 (Haines 1977; Sellars 1997).

Roundups and confinement of bison in northern Yellowstone ceased in 1938, and during the 1940s, managers decided these bison should live in a more natural state like other wildlife (Cahalane 1944; Sellars 1997; Knudten 2011). However, managers continued to feed bison during winter until 1952, when ranching operations in the Lamar Valley were discontinued and bison were allowed to move freely within the park (Meagher 1973). Managers recognized that without supplemental feeding the bison in northern Yellowstone would disperse more widely and eventually be subject to hunting outside the park (Cahalane 1944; Meagher 1973). However, this shift in management philosophy was deemed necessary to restore wild bison, as opposed to perpetuating “a semi-domesticated cattle herd” like on a ranch or game farm (Cahalane 1944).

The indigenous, remnant bison in the Pelican Valley of central Yellowstone gradually increased in numbers once protected from poaching (Meagher 1973). To stimulate population growth and disperse bison more widely across existing habitat, park managers relocated 71 bison from northern Yellowstone to the Firehole River drainage and Hayden Valley in the central region of the park during 1936 (Cahalane 1944). Bison numbers increased during the 1940s and there were more than 700 bison in central Yellowstone by 1949. Bison soon began to move back-and-forth between the Firehole River drainage and Hayden Valley areas (Meagher 1973). Most of these bison spent summer in the Hayden Valley, with some use of the Madison Plateau, through the mid-1950s (Meagher 1973). Many bison from the Hayden Valley moved westward across the Mary Mountain divide to spend winter in the "Firehole geyser basin," where snow depths were lower due to geothermal influences (Meagher 1998; Taper et al. 2000 provides maps and descriptions of the spatial distribution of bison over time). However, there was little mixing between these relocated bison and the indigenous bison in the Pelican Valley until the 1950s (Meagher 1998; Gates and Broberg 2011).

As early as the 1920s, park managers became concerned about brucellosis and overgrazing by bison and other ungulates, especially elk. The Secretary of the Interior is authorized to dispose of "surplus" bison (16 USC § 36) and destroy animals that may be detrimental to parks (16 USC § 3). Brucellosis can be considered detrimental to Yellowstone bison because it induces abortions and limits tolerance for their migration to low-elevation winter ranges in Montana (Franke 2005; Plumb et al. 2009). Park managers used these authorities to implement periodic removals of bison from northern Yellowstone during 1925 to 1966 and central Yellowstone during 1954 to 1966 to reduce numbers and remove individuals exposed to brucellosis (Barmore 1968; Meagher 1973). Many hundreds of live bison were shipped to zoos, parks, tribal reservations, and other places (Cahalane 1944). Thousands of bison were killed and provided to American Indian tribes, relief agencies, and contract sales (Skinner and Alcorn 1942; Meagher 1973). By 1967, there were less than 100 bison in northern Yellowstone and 400 bison in central Yellowstone (Fuller et al. 2007a).

## Bison as Wildlife, Contributing to Ecological Processes

In 1968, managers ceased the culling of bison in Yellowstone National Park, and allowed numbers to fluctuate in response to predators, resource limitations, and weather (Cole 1971; Houston 1982; National


NPS/Neal Herbert

*Lone bison in the northern region of Yellowstone National Park.*

Research Council 2002). Bison numbers increased under this new management paradigm and hundreds of animals from the central and northern regions of the park began to migrate and expand their ranges towards the boundary (Meagher 1989b, 1998; Cannon 2001; Meagher et al. 2002; Bruggeman et al. 2009c). During the 1970s, bison from northern Yellowstone expanded their range westward from the Lamar Valley and down the elevation gradient formed by the Yellowstone River (Meagher 1989b). Subsequently, some bison began to spend portions of the summer in the Lamar Valley and along lower Slough Creek and Soda Butte Creek, rather than migrating to higher elevations (Meagher et al. 2002). Beginning in the 1980s, bison in central Yellowstone began moving west from the Pelican Valley to the northern shore of Yellowstone Lake and into the Hayden Valley during winter (Meagher 1998). Subsequently, more bison began moving earlier from the Hayden Valley west to the "Firehole geyser basin," and eventually, into the Madison Valley where some bison remained during summer (Meagher 1998; Meagher et al. 2002; Bruggeman et al. 2009c). During a few winters in the 1980s and 1990s, bison began moving from the Madison Valley in west-central Yellowstone toward the northern boundary of the park (Meagher et al. 2002). These movements increased during the 2000s (Clarke et al. 2005; Fuller et al. 2007a). Concurrent with these westward and northern shifts, the summer distribution of bison from Pelican Valley changed, with bison no longer migrating across the Mirror Plateau to the upper Lamar Valley after the mid-1980s (Meagher et al. 2002). Instead, more bison stayed in the Hayden Valley and mingled with bison from the Mary Mountain area (previously relocated from northern Yellowstone in 1936) during summer and autumn (Meagher 1998; Taper et al. 2000). Over time, intermixing between these bison increased (Meagher 1998).

Attempts to deter movements by bison outside Yellowstone National Park and into Montana during winter failed (Meagher 1989a,b). As a result, the occasional bison that left the park during 1967 to 1984 were killed by Montana game wardens or National Park Service personnel to prevent the possible transmission of brucellosis from bison to cattle (MFWP and MDOL 2004). Montana Fish, Wildlife & Parks subsequently managed a state-licensed hunt for bison until 1991 (MFWP and MDOL 2004). As the number of bison migrating outside the boundary of Yellowstone National Park increased, the National Park Service agreed to control bison near the boundary of the park and a series of management plans were developed to define specific boundaries and lethal control measures (USDI, NPS and USDA, USFS, APHIS 2000a,b). About 3,100 bison were culled from the population during 1985 through 2000 when they attempted to migrate outside the park (White et al. 2011). This total included 2,339 bison that were captured and shipped to meat processing facilities and 778 bison that were shot by hunters or state livestock or wildlife personnel (White et al. 2011). These migrations and culls generated intense controversy among environmentalists, stock growers, and management agencies regarding issues of bison conservation and disease containment (Cheville et al. 1998).

## Interagency Bison Management Plan

The management of bison outside Yellowstone National Park is the prerogative of surrounding states and the U.S. Forest Service on National Forest System lands. Differences in legal classifications and management authorities among these governments and various agencies can lead to jurisdictional challenges in bison management (Plumb et al. 2009; Becker et al. 2013). Even though bison are the state mammal of Wyoming, they are considered livestock everywhere except in specific hunting areas adjacent to Grand Teton and Yellowstone national parks. In fact, the Wyoming Game and Fish Department does not support the establishment of wild bison populations outside national parks and refuges (Talbott 2014). The wildlife conservation strategy for Idaho mentions bison as a species of concern, but state agricultural regulations do not recognize wild bison and consider them livestock (Idaho Department of Fish and Game 2005). The Montana Legislature has designated Yellowstone bison as a species requiring disease control because the population is chronically infected with brucellosis.

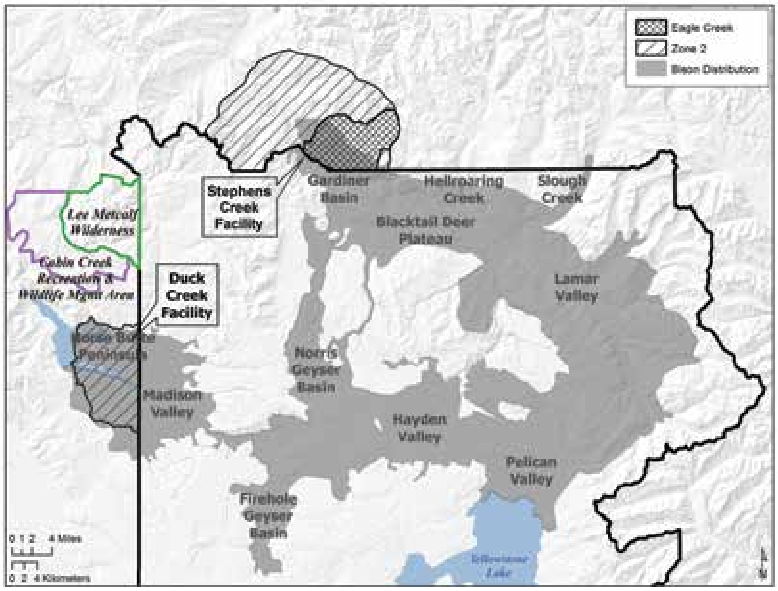


*Figure 3.1. Conservation areas for bison in and near Yellowstone National Park under the 2000 Interagency Bison Management Plan, as adjusted. Zone 2 depicts areas where there is tolerance for some bison in Montana during winter.*

As a result, the Department of Livestock is the lead agency for managing wild bison that migrate into Montana, and can remove animals that jeopardize compliance with livestock disease control programs (81-2-120 [1-4] Montana Code Annotated; Administrative Rules of Montana 32.3.224). The Montana Legislature also decided that Yellowstone bison pose a threat of brucellosis transmission to people or cattle, and for damage to persons or property (87-1-216 [1] Montana Code Annotated). As a result, Montana Fish, Wildlife & Parks is required to cooperate with the Department of Livestock in managing bison, including administering public hunts on lands adjacent to Yellowstone National Park (87-1-216 Montana Code Annotated). Elsewhere in the state, Montana Fish, Wildlife & Parks does not support free-ranging bison that are not contained by fencing or some other barrier (Brown 2014; French 2014). Similar biases, designations, and regulations do not exist for elk that are also chronically infected with brucellosis.

In 2000, the federal government and the State of Montana agreed to guidelines for cooperatively managing the risk of brucellosis transmission from bison to cattle (Plumb et al. 2009). This Interagency Bison Management Plan also emphasized conserving the wild bison population and allowing some bison to occupy winter ranges on public lands in Montana (USDI, NPS and USDA, USFS, APHIS 2000a,b; Figure 3.1). Five agencies were originally responsible for implementing the plan—the National Park Service, Animal and Plant Health Inspection Service, U.S. Forest Service, Montana Fish, Wildlife & Parks, and the Montana Department of Livestock. The Confederated Salish and Kootenai Tribes of the Flathead Nation, Nez Perce Tribe, and the InterTribal Buffalo Council were added as partners in 2009 due to their treaty hunting rights on open and unclaimed federal lands in Montana and their commitment to reestablishing bison herds on tribal lands.

The Interagency Bison Management Plan was designed to progress through a series of management steps that initially tolerated only bison testing negative for exposure to *Brucella* bacteria on winter ranges outside Yellowstone National Park, but eventually tolerated untested bison when cattle were not present (USDI, NPS and USDA, USFS, APHIS 2000a,b). During step 1, the agencies agreed to (White et al. 2011):

- Enforce spatial and temporal separation between bison and cattle;
- Use hazing by humans on horseback, all-terrain vehicles, or in helicopters to prevent bison movements from Yellowstone National Park;
- If hazing was unsuccessful, capture bison attempting to leave the park and test them for brucellosis exposure;
- Send bison testing positive to meat processing facilities;
- Vaccinate non-pregnant bison testing negative;
- Hold bison testing negative at the north boundary for release back into the park in spring;


*Staff on horseback hazing bison in the Gardiner basin near the northern boundary of Yellowstone National Park.*

NPS/Neal Herbert

*Bison feeding at Swan Lake Flat in Yellowstone National Park.*

- Release up to 100 bison testing negative at the west boundary and allow them to use habitat adjacent to the park until May 15;
- Conduct research on *Brucella* persistence in the environment to determine an adequate temporal separation period between bison and cattle;
- Conduct research on the safety and efficacy of strain RB51 vaccine;
- Develop and evaluate a remote vaccine delivery system; and
- Encourage and, if necessary, mandate the vaccination of female cattle greater than 4 months of age that might graze on winter ranges used by bison.

Step 2 was to begin when cattle no longer grazed during winter on the Royal Teton Ranch, just north of the park boundary in the Gardiner basin. Management actions initiated in step 1 were continued, except up to 100 bison testing negative for brucellosis exposure would be released at the north boundary and allowed to use habitat adjacent to the park until April 15. Also, any calf and yearling bison that could not be captured at the west boundary would be vaccinated using a remote delivery system.

Step 3 was to begin once the agencies determined an adequate temporal separation period between bison and cattle, gained experience in managing bison outside the park, and initiated a vaccination program for all female bison in the population. The agencies would tolerate up to 100 untested bison in both the north and west boundary areas, use capture and culling in these areas to maintain the population near 3,000 bison, and ensure no bison were outside the park after the spring cut-off dates. The agencies also agreed to develop a quarantine protocol for certifying test-negative bison as brucellosis free.

## Adaptive Management Adjustments

The Interagency Bison Management Plan was adjusted in 2005 and 2006 to include bison hunting as a management action outside Yellowstone National Park and increase tolerance for bull bison because there is virtually no risk of them transmitting brucellosis to cattle (Clarke et al. 2005; Interagency Bison Management Plan Partner Agencies 2006). These adjustments allowed bison not tested for brucellosis exposure to migrate to winter ranges outside the park and provide hunting opportunities. Since 2005, Montana Fish, Wildlife & Parks has administered a bison hunt between November 15 and February 15 on lands adjacent to the park. The intent is to hunt wild bison under fair chase conditions and reduce damage to private property by altering bison behavior and distribution (MFWP and MDOL 2004). In 2006, Montana recognized the treaty rights of the Confederated Salish and Kootenai Tribes of the Flathead Nation and the Nez Perce Tribe for harvesting bison on open and unclaimed federal lands adjacent to the park (MFWP 2006a,b). In 2009 and 2010, Montana also recognized the treaty rights of the Shoshone-Bannock Tribes and the Confederated Tribes of the Umatilla Indian Reservation to hunt bison on these lands (MFWP 2009, 2010b).

*By 1894, bison in and adjacent to the northern region of Yellowstone had been extirpated, and only about 23 bison were left in the Pelican Valley of central Yellowstone by 1901.*

Public and treaty hunters harvest variable numbers of bison each year depending on the timing and extent of bison migration into Montana (White et al. 2011; Canfield et al. 2012; Jones et al. 2012; Clarke et al. 2014a). Starting in 2007, Montana Fish, Wildlife & Parks set a state quota of 44 either-sex licenses allocated between hunting districts in the Gardiner and West Yellowstone areas, with up to 100 additional female–calf permits issued incrementally if warranted by conditions. An increase in these quotas is expected in 2015. The tribes develop and enforce their own harvest regulations, and there is no defined limit on the number or type (age, sex) of bison the tribes may harvest (MFWP and MDOL 2013). However, federal, state, and tribal managers meet each summer to discuss objectives, no-shooting zones, access, enforcement, and the sharing of harvest data (Interagency Bison Management Plan Members 2013).

In addition, Montana Fish, Wildlife & Parks and the U.S. Department of Agriculture, Animal and Plant Health Inspection Service (2006) conducted a quarantine feasibility study during 2005 to 2010 with 214 Yellowstone bison calves that initially tested negative for brucellosis exposure. These bison were held at a research facility north of Yellowstone National Park to evaluate if they would remain free of brucellosis through at least their first pregnancy and calving. The study was successful and the surviving original bison and their offspring were declared brucellosis free (MFWP 2010a, 2011; Clarke et al. 2014b). In February 2010, 87 bison were transferred from the quarantine facility to the Green Ranch in Montana, owned by Turner Enterprises, Inc., for five years of additional surveillance. In November 2014, the original quarantine bison plus about 25 percent of their offspring were transferred to the Fort Peck Indian Reservation in Montana. The rest of the bison were retained by Turner Enterprises. In March 2012, Montana transferred 61 bison from the quarantine facility to the Fort Peck Indian Reservation for five years of additional surveillance (MFWP 2011). Thirty-four of these bison were subsequently transferred to the Fort Belknap Reservation in Montana.

Despite these successes, progress was initially slow in completing the Interagency Bison Management Plan's three successive steps to incrementally increase tolerance for bison moving outside the park (White et al. 2011). Also, more than 1,000 bison (21 percent) were removed from the population during winter 2006 and more than 1,700 bison (37 percent) were removed during winter 2008 because hazing was no longer effective at keeping them in agreed-upon management areas (White et al. 2011; Table 3.1). In 2006, 917 bison were captured and shipped to meat processing facilities, 40 were shot by hunters, and 87 were captured and shipped to a quarantine facility. In 2008, 1,448 bison were shipped to processing facilities, 166 were harvested, and 112 were shipped to quarantine. These culls removed a disproportionately large number of females and reduced population growth—similar to the effects of culls during earlier decades under different management strategies (Meagher 1973; Halbert 2003; White et al. 2011; Treanor et al. 2013; Table 3.2). The federal government and the State of Montana were criticized for these culls and for not consistently defining measurable objectives or applying adaptive management principles (Holling 1978; U.S. Government Accountability Office 2008). In response, the partners made several adjustments to the plan based on prevailing

| Winter | Maximum no. bison counted previous July-August | | | Sent to slaughter/management culls | | Hunter harvest[a] | | Sent to quarantine | | Total | Age and gender composition of culls/harvests | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | North | Central | Total | North | West | North | West | North | West | | Male | Female | Calf | Unknown |
| 1970-84 | | | | 0 | 0 | 13 | 0 | 0 | 0 | 13 | 4 | 7 | 0 | 2 |
| 1985 | 695 | 1,552 | 2,247 | 0 | 0 | 88 | 0 | 0 | 0 | 88 | 42 | 37 | 8 | 1 |
| 1986 | 742 | 1,609 | 2,351 | 0 | 0 | 41 | 16 | 0 | 0 | 57 | 42 | 15 | 0 | 0 |
| 1987 | 998 | 1,778 | 2,776 | 0 | 0 | 0 | 7 | 0 | 0 | 7 | 5 | 2 | 0 | 0 |
| 1988 | 940 | 2,036 | 2,976 | 0 | 0 | 2 | 37 | 0 | 0 | 39 | 27 | 7 | 0 | 5 |
| 1989 | NA[b] | NA[b] | NA[b] | 0 | 0 | 567 | 2 | 0 | 0 | 569 | 295 | 221 | 53 | 0 |
| 1990 | 592 | 1,885 | 2,477 | 0 | 0 | 1 | 3 | 0 | 0 | 4 | 0 | 0 | 0 | 4 |
| 1991 | 818 | 2,203 | 3,021 | 0 | 0 | 0 | 14 | 0 | 0 | 14 | 0 | 0 | 0 | 14 |
| 1992 | 822 | 2,290 | 3,112 | 249 | 22 | 0 | 0 | 0 | 0 | 271 | 113 | 95 | 41 | 22 |
| 1993 | 681 | 2,676 | 3,357 | 0 | 79 | 0 | 0 | 0 | 0 | 79 | 9 | 8 | 9 | 53 |
| 1994 | 686 | 2,635 | 3,321 | 0 | 5 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 5 |
| 1995 | 1,140 | 2,974 | 4,114 | 307 | 119 | 0 | 0 | 0 | 0 | 426 | 77 | 66 | 31 | 252 |
| 1996 | 866 | 3,062 | 3,928 | 26 | 344 | 0 | 0 | 0 | 0 | 370[c] | 100 | 71 | 10 | 189 |
| 1997 | 785 | 2,593 | 3,378 | 725 | 358 | 0 | 0 | 0 | 0 | 1,083[d] | 329 | 330 | 144 | 280 |
| 1998 | 455 | 1,715 | 2,170 | 0 | 11 | 0 | 0 | 0 | 0 | 11 | 0 | 0 | 0 | 11 |
| 1999 | 493 | 1,399 | 1,892 | 0 | 94 | 0 | 0 | 0 | 0 | 94 | 44 | 49 | 1 | 0 |
| 2000 | 540 | 1,904 | 2,444 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2001 | 508 | 1,924 | 2,432 | 0 | 6 | 0 | 0 | 0 | 0 | 6 | 6 | 0 | 0 | 0 |
| 2002 | 719 | 2,564 | 3,283 | 0 | 202 | 0 | 0 | 0 | 0 | 202 | 60 | 42 | 16 | 84 |
| 2003 | 813 | 2,902 | 3,715 | 231 | 13 | 0 | 0 | 0 | 0 | 244 | 75 | 98 | 43 | 28 |
| 2004 | 888 | 2,923 | 3,811 | 267 | 15 | 0 | 0 | 0 | 0 | 282 | 58 | 179 | 23 | 22 |
| 2005 | 876 | 3,339 | 4,215 | 1 | 96 | 0 | 0 | 0 | 17 | 114 | 23 | 54 | 20 | 17 |
| 2006 | 1,484 | 3,531 | 5,015 | 861 | 56 | 32 | 8 | 87 | 0 | 1,044 | 205 | 513 | 245 | 81 |
| 2007 | 1,377 | 2,512 | 3,889 | 0 | 4 | 47 | 12 | 0 | 0 | 63 | 53 | 6 | 0 | 4 |
| 2008 | 2,070 | 2,624 | 4,694 | 1,288 | 160 | 59 | 107 | 112 | 0 | 1,726 | 516 | 632 | 332 | 246 |
| 2009 | 1,500 | 1,469 | 2,969 | 0 | 4 | 1 | 0 | 0 | 0 | 5 | 5 | 0 | 0 | 0 |
| 2010 | 1,839 | 1,462 | 3,301 | 3 | 0 | 4 | 0 | 0 | 0 | 7 | 7 | 0 | 0 | 0 |
| 2011 | 2,245 | 1,653 | 3,898 | 6 | 0 | Unk | Unk | 53 | 0 | 260 | 106 | 102 | 52 | 0 |
| 2012 | 2,314 | 1,406 | 3,720 | 0 | 0 | 15 | 13 | 0 | 0 | 28 | 14 | 12 | 2 | 0 |
| 2013 | 2,669 | 1,561 | 4,230 | 0 | 0 | 148 | 81 | 0 | 0 | 229 | 116 | 85 | 28 | 4 |
| 2014 | 3,420 | 1,504 | 4,924 | 258 | 0 | 258 | 64 | 60 | 0 | 640 | 200 | 284 | 152 | 4 |

*Table 3.1. Annual removals of Yellowstone bison through harvests and management culls from the northern and western management areas in Yellowstone National Park and nearby areas of Montana during winter (White et al. 2010, Geremia et al. 2014b).*

| Central region | | | |
|---|---|---|---|
| | Abundance | Males:100 females | Juveniles:100 adults |
| 2003 | 2,924 (2,768-3,084) | 60 (53-68) | 40 (36-44) |
| 2004 | 3,396 (3,225-3,572) | 110 (99-124) | 34 (31-37) |
| 2005 | 3,437 (3,281-3,595) | 89 (80-99) | 40 (36-43) |
| 2006 | 2,422 (2,297-2,556) | 112 (100-126) | 35 (32-38) |
| 2007 | 2,825 (2,680-2,974) | 82 (73-92) | 43 (39-47) |
| 2008 | 1,379 (1,305-1,460) | 101 (89-115) | 26 (23-28) |
| 2009 | 1,509 (1,428-1,592) | 116 (103-132) | 30 (27-33) |
| 2010 | 1,690 (1,600-1,785) | 126 (111-143) | 31 (28-34) |
| 2011 | 1,380 (1,302-1,459) | 147 (129-166) | 26 (24-29) |
| 2012 | 1,584 (1,503-1,674) | 129 (114-145) | 28 (26-31) |
| 2013 | 1,367 (1,296-1,443) | 127 (113-145) | 29 (26-32) |

| Northern region | | | |
|---|---|---|---|
| | Abundance | Males:100 females | Juveniles:100 adults |
| 2003 | 895 (847-945) | 96 (85-110) | 33 (29-35) |
| 2004 | 1,086 (1,013-1,148) | 85 (77-96) | 36 (32-39) |
| 2005 | 1,308 (1,244-1,371) | 86 (77-96) | 34 (30-37) |
| 2006 | 1,275 (1,211-1,342) | 75 (66-84) | 45 (41-50) |
| 2007 | 1,807 (1,712-1,908) | 52 (46-59) | 47 (42-53) |
| 2008 | 1,586 (1,507-1,669) | 87 | 47 |
| 2009 | 1,674 (1,590-1,765) | 101 (93-118) | 42 (38-46) |
| 2010 | 1,910 (1,813-2,016) | 60 (54-68) | 53 (47-60) |
| 2011 | 2,296 (2,177-2,425) | 61 (54-68) | 45 (40-49) |
| 2012 | 2,583 (2,458-2,720) | 66 (58-75) | 60 (53-68) |
| 2013 | 3,204 (3,040-3,371) | 63 (57-71) | 56 (50-62) |

*Table 3.2. Estimated average and 95 percent range for the age and sex structure of bison in the central and northern regions of Yellowstone National Park during 2003 through 2013 (Geremia et al. 2013).*

conditions and developed a long-term monitoring and research program to guide decision making (USDI, NPS et al. 2008; White et al. 2014). These adjustments (1) further described the circumstances for bison occupying habitats outside the park, (2) established a precedent for minimizing the shipment of bison to meat processing facilities, (3) re-affirmed the commitment to vaccinating bison, (4) outlined a process for sharing decision documents with the public, and (5) specified metrics for annual monitoring and reporting on management actions (USDI, NPS et al. 2008).

In 2009, an agreement with a private landowner removed livestock from the Royal Teton Ranch for 30 years to allow bison to access and use habitats north of the park, including portions of the ranch and the Gallatin National Forest (MFWP 2008a,b; NPS and MFWP 2008). This agreement led to adjustments to the Interagency Bison Management Plan in 2011 and 2012 that increased tolerance for untested bison north and west of the park (MFWP and MDOL 2012). During 2011 through 2014, 200 to 1,100 bison migrated to habitat in the Hebgen and Gardiner basins of Montana during winter (Canfield et al. 2012; Jones et al. 2012; Clarke et al. 2014a).

In 2010, the partners supported the organization of a working group comprised of people from a diverse group of stakeholders to develop collaborative ideas for managing Yellowstone bison. This Citizens Working Group on Yellowstone Bison (2011) provided numerous recommendations to bison managers regarding brucellosis risk reduction, bison population management, and bison habitat. Most of these recommendations were subsequently implemented as part of the adaptive management plan (Jones et al. 2012). In return, the partners involved with the Interagency Bison Management Plan provided the working group and other interested citizenry with periodic updates on the real impacts of bison and brucellosis management actions compared to their anticipated effects. Through this framework, the partners made adaptive management adjustments transparent and accountable to stakeholders by: (1) soliciting public comment on adaptive adjustments being considered by decision-makers, (2) posting


*A bison grazes outside of the historic Yellowstone Lake Hotel.*

monitoring reports on websites for the Interagency Bison Management Plan (http://ibmp.info) and Yellowstone National Park (http://www.nps.gov/yell/naturescience/bison.htm), (3) holding public information meetings, (4) publishing scientific articles, and (5) conducting necessary analyses.

## Conclusions

Moving forward, the extent to which bison can ultimately use the Greater Yellowstone Area will be defined by the tolerance of modern society (Lott 2002; Franke 2005; Plumb et al. 2009; Bailey 2013). The degree of tolerance will likely depend on active management to mediate conflicts between bison and humans—which is consistent with large mammal conservation programs worldwide where agriculture and urbanization surround nature preserves (Plumb et al. 2009). Though such management upsets some people, it has necessarily occurred since the early part of the past century. In fact, human influences on bison behavior and demography extend much further back in time. For example, humans have been a significant predator on bison for many centuries, as evidenced by kill sites in the Paradise Valley north of Yellowstone National Park that were used repeatedly over time (Cannon 2001).


*Bison moving north on U.S. Route 89 outside of Yellowstone National Park.*


NPS/Jim Peaco

*Bison moving in single file through unbroken snow near Tower Junction in the northern region of Yellowstone National Park.*

# Chapter 4

## SEASONAL DISTRIBUTIONS AND MOVEMENTS

*Chris Geremia, P.J. White, Rick L. Wallen, and Douglas W. Blanton*

Yellowstone bison can move long distances in relatively short periods of time—occasionally traveling more than 30 kilometers (19 miles) in a single day and annually ranging over areas of 100 to 750 square kilometers (39 to 290 square miles; Meagher 1989b; Geremia et al. 2011, 2014b). They are considered migratory because most animals move back and forth between seasonal ranges to better access food resources (Senft et al. 1987; Mueller and Fagan 2008; Plumb et al. 2009). They have also dispersed between areas and expanded their winter ranges in recent decades. Dispersal refers to long-lasting or permanent movements by animals from one area to another, while range expansion is the movement of animals beyond the limits of the traditional distribution for a population (Gates and Larter 1990; Gates and Broberg 2011).

## Migration and Dispersal

The primary factors influencing bison migrations are: (1) seasonal vegetation changes that affect food quality, (2) the breeding season, (3) the distribution, size, and quality of foraging sites, and (4) snow accumulation that affects energy expenditures and access to food (Meagher 1973; Bruggeman et al. 2009b; Gates and Broberg 2011; Geremia et al. 2011, 2014b). Most bison show fidelity to seasonal ranges that are more than 50 square kilometers (19 square miles) in size and dominated by grassland and shrub steppe habitats. Individual bison do not segregate into territories, but tend to aggregate into dynamic groups that form, merge, and break-up as individuals feed, rest, and move across the landscape. Group movements are correlated, with associations of groups making back-and-forth movements across and between seasonal ranges over a span of days.[5]

As mentioned in Chapter 3, bison in the northern region of Yellowstone National Park traditionally spent summer on the Mirror Plateau and slopes of the Absaroka Mountains along the eastern boundary, but spent winter in the Lamar or Pelican valleys (Meagher 1973). However, progressive changes began in the mid-1970s when groups began to move west and travel downslope along the Yellowstone River and parallel road corridor to the Blacktail Deer Plateau and Gardiner basin during winter (Meagher 1989b). As the number of bison in northern Yellowstone increased, more bison spent summer on the traditional wintering area of the Lamar Valley, which increased the magnitude and extent of seasonal movements to lower-elevation areas (Meagher 1989b).

Bison in central Yellowstone traditionally spent summer in the Pelican or Hayden valleys and on the Mirror Plateau and upper Lamar River drainage (Meagher 1973). They spent winter in these valleys or the lower-elevation Firehole River drainage (Meagher 1973). For decades, bison rarely moved between the Hayden and Pelican valleys during any time of the year (Meagher 1973, 1989b). During the winter of 1982, however, groups of bison moved through the Pelican Valley to

5 Portions of this chapter were adapted from Geremia et al. (2011, 2014b).

the northern shore of Yellowstone Lake and into the Hayden Valley (Meagher 1998). In subsequent years, regular movements between the Hayden and Pelican valleys increased and bison that spent winter in the Pelican Valley stopped moving to the Mirror Plateau during summer (Meagher 1998). More bison began moving west from the Hayden Valley to the Firehole River drainage, and eventually, into the Madison Valley (Meagher 1998; Bruggeman et al. 2009c). By 1995, some bison from central Yellowstone made movements towards northern Yellowstone along the river and roadway corridor connecting Mammoth Hot Springs and the interior of the park (Taper et al. 2000). By 2005, more than 1,000 bison from central Yellowstone moved to the northern region of the park during winter. During subsequent winters, many of these animals were captured and shipped to meat processing facilities after attempting to cross the northern boundary of the park into Montana (White et al. 2011). The remaining bison either stayed in northern Yellowstone or continued to seasonally migrate between the central and northern regions of the park (Geremia et al. 2011, 2014b).

Dispersal movements and range expansion by Yellowstone bison were often associated with severe snow events that interacted with bison density to limit nutritional intake and foraging efficiency (Meagher 1989b, 1998; Coughenour 2005; Plumb et al. 2009). Changes in distribution and seasonal movements continued as bison numbers increased, and eventually led bison to expand their winter range to lower-elevation areas outside the park boundary (Taper et al. 2000; Gates and Broberg 2011). Prior experience with particular routes and new foraging areas likely contributed to a rapid increase in movements by large numbers of bison during subsequent winters, even when snow conditions were relatively mild (Meagher 1989b; Geremia et al. 2011, 2014b).

Range expansion can delay responses to food limitations since new ranges provide additional forage (Larter and Gates 1990). As a result, increases in winter range areas used by Yellowstone bison from 1976 onwards contributed to sustained population growth in both the central and northern regions of the park (Taper et al. 2000;


*Bison spread across Yellowstone's Lamar Valley.*

Coughenour 2005; Plumb et al. 2009). However, culling and hazing bison back into the park to reduce the risk of brucellosis transmission to cattle in Montana limited range expansion by bison much beyond the boundary of Yellowstone National Park (Gates and Broberg 2011; White et al. 2011). Without this intensive management intervention, bison almost certainly would have continued to disperse to suitable habitat areas further outside the park (Plumb et al. 2009; Gates and Broberg 2011).

## Seasonal Movements

During summer, bison in northern Yellowstone are concentrated in an approximately 40-kilometer (25-mile) long region along the Lamar River from Cache Creek in the east towards the confluence of the Yellowstone River in the west (Geremia et al. 2014b; Figure 4.1). A portion of these bison make prolonged forays to the high-elevation Specimen Ridge and Mirror Plateau areas, with occasional trips to the Pelican and Hayden valleys. Bison from central Yellowstone return to the Hayden Valley from wintering areas in western and northern Yellowstone, with nearly all animals in the Hayden Valley during July and August. In late summer, large numbers of these bison travel back and forth between the Hayden Valley, northern shore of Yellowstone Lake, and the Pelican Valley (Geremia et al. 2014b; Figure 4.1).

In early autumn, bison make brief trips from summer ranges to most winter ranges, with nearly all animals subsequently returning to the summer range (Figure 4.2). These exploratory trips may enable bison to assess food availability across winter ranges or access remaining high-quality food prior to vegetation becoming older and dying (Geremia et al. 2014b).

As winter progresses, bison in northern Yellowstone move downslope to the lower Yellowstone River drainage (Tower, Slough Creek, Hellroaring) and Blacktail Deer Plateau. From there, bison may move further northwest to the lower-elevation Gardiner basin where snow pack is lower and new vegetation growth begins earlier in spring (Geremia et al. 2014b; Figure 4.3). These movements are

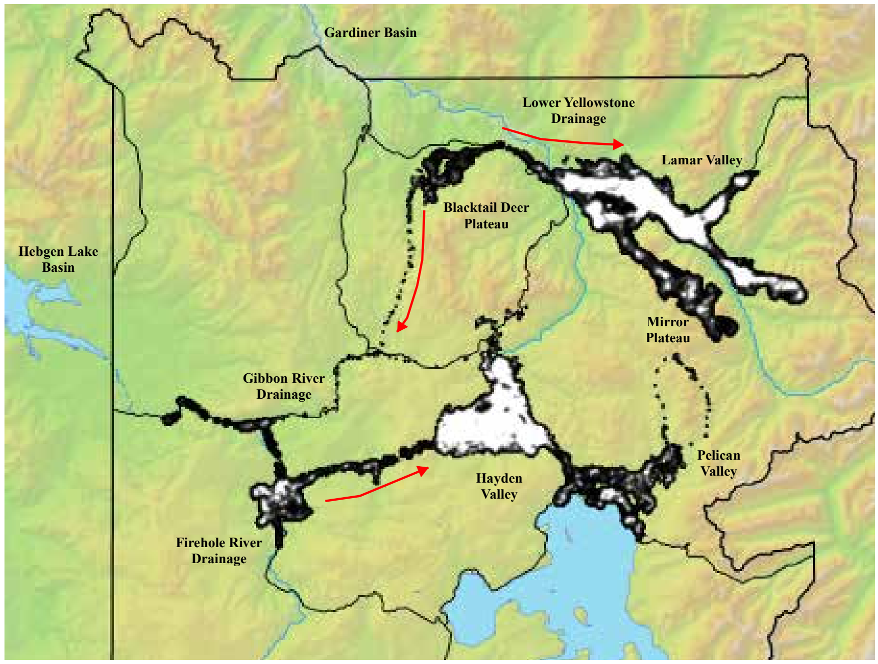


*Figure 4.1. Summer (June-August) utilization distribution of locations from 66 radio-collared, adult, female bison in Yellowstone National Park during 2004 through 2012, with white areas showing increased use and arrows showing the direction of most movements.*

made along several pathways that follow the Yellowstone and Gardner rivers. Bison often make brief return trips to higher-elevation winter ranges before returning to lower elevations.

Bison in central Yellowstone leave the summer range and move to northern Yellowstone following the river and roadway corridor, or to western Yellowstone following a historic migration route (Mary Mountain pass) that connects the Hayden Valley and Firehole River drainage (Bjornlie and Garrott 2001; Geremia et al. 2014b; Figures 4.2 and 4.3). From the Firehole River drainage, bison move downslope to access several meadows along the Firehole, Gibbon, and Madison rivers. Movements are relatively fluid between these meadows, with short stays in any given meadow. Bison in central Yellowstone predominantly access northern Yellowstone using the river and roadway corridor that connects the Gibbon Canyon with Mammoth Hot

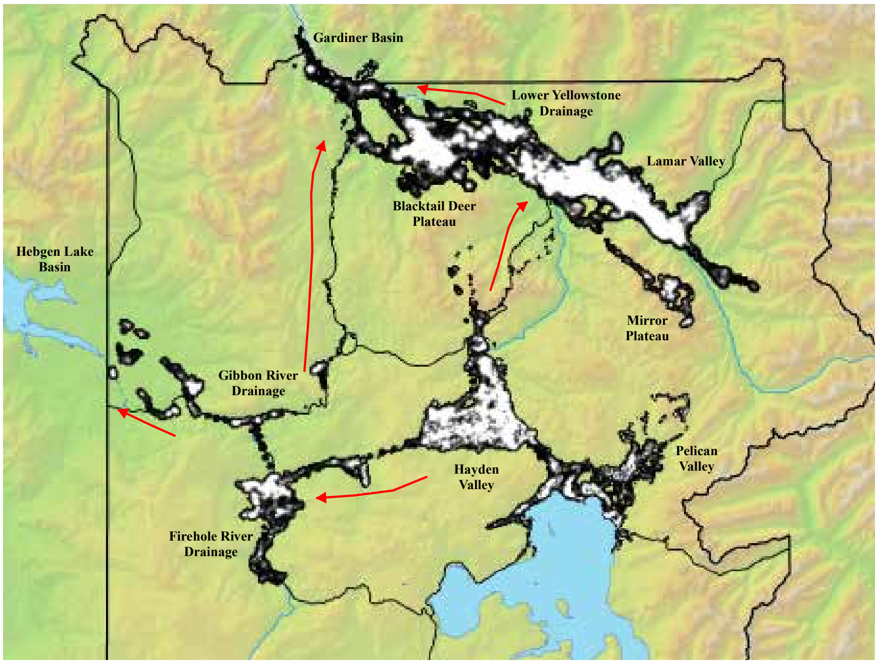


*Figure 4.2. Autumn (September-November) utilization distribution of locations from 66 radio-collared, adult, female bison in Yellowstone National Park and nearby areas of Montana during 2004 through 2012, with white areas showing increased use and arrows showing the direction of most movements.*

Springs. Some of these bison gradually move upslope to the Blacktail Deer Plateau and lower Yellowstone River drainage, before moving to lower-elevation wintering areas in the Gardiner basin (Geremia et al. 2014b; Figure 4.3).

Movement patterns are reversed in spring as snow melts and bison follow new vegetation growth from lower to higher elevations (Frank and McNaughton 1993; Frank et al. 2013; Wilmers et al. 2013; Geremia et al. 2014b). The onset of new vegetation growth typically begins three weeks earlier in northern Yellowstone than in central Yellowstone (Thein et al. 2009). Thus, return movements occur earlier in northern Yellowstone and coincide with the time when many bison in central Yellowstone are just reaching low-elevation wintering areas along the Madison River and eastern portion of Hebgen Lake outside the western boundary of the park (Geremia et al. 2014b; Figure 4.4).

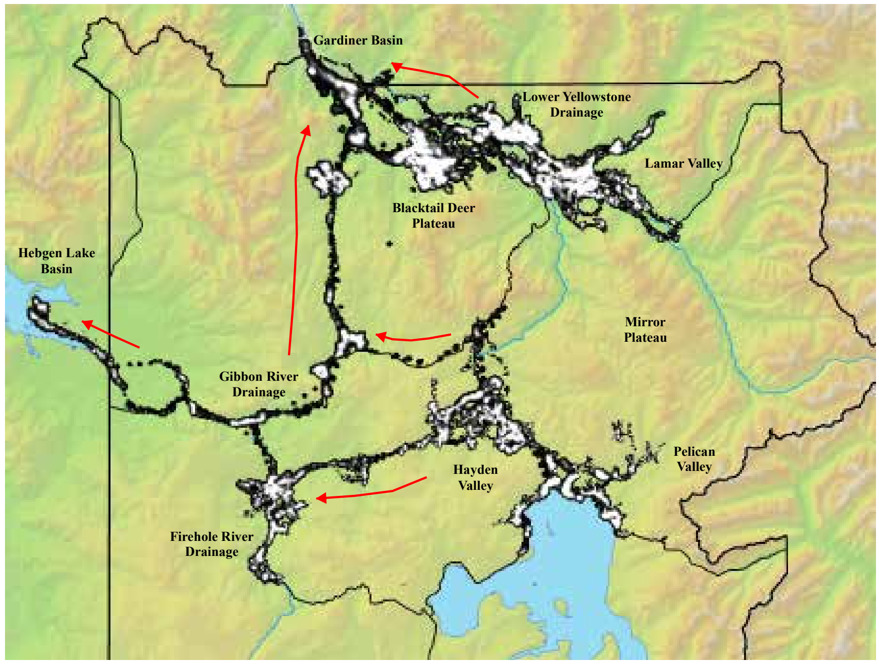


*Figure 4.3. Winter (December-February) utilization distribution of locations from 66 radio-collared, adult, female bison in Yellowstone National Park and nearby areas of Montana during 2004 through 2012, with white areas showing increased use and arrows showing the direction of most movements.*

Emergence of new vegetation in the Hebgen Lake basin coincides with the calving period for bison, and several hundred bison move to this winter range at this time. These animals remain in this area during calving, before returning to higher-elevation summer ranges inside Yellowstone National Park over the course of several days or weeks during June.

## Seasonal Movement Strategies

As numbers of bison increase, the abundance of bison and other grazing ungulates may become sufficient to elicit increased competition for key resources (Coughenour 2005; Plumb et al. 2009; Frank et al. 2013). Decreased food resources or foraging efficiency provide an impetus for bison to move (Coughenour 2005; Gates and Broberg 2011). Annual forage production and snow pack also influence food

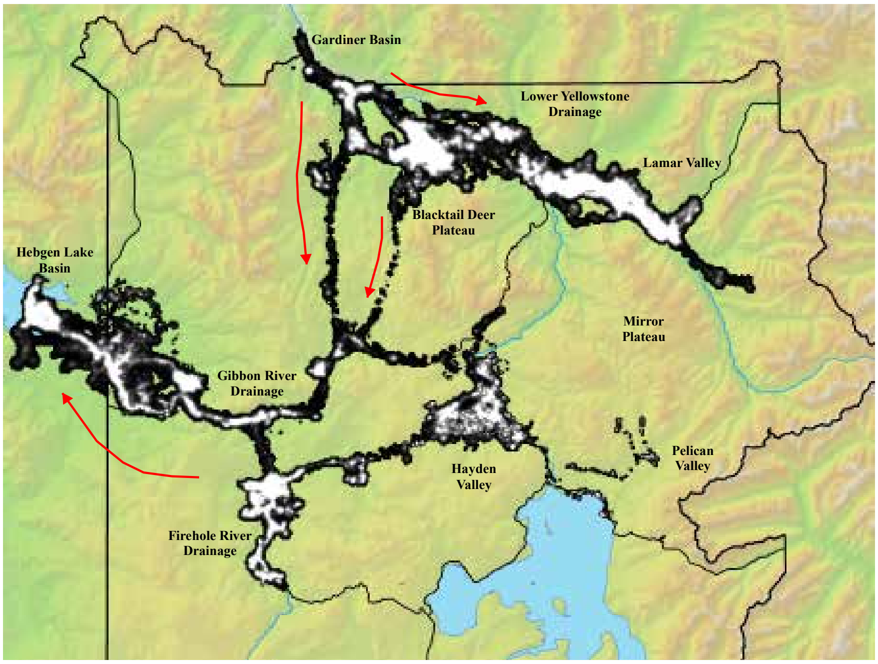


*Figure 4.4. Spring (March-May) utilization distribution of locations from 66 radio-collared, adult, female bison in Yellowstone National Park and nearby areas of Montana during 2004 through 2012, with white areas showing increased use and arrows showing the direction of most movements.*

availability, foraging efficiency, and movements (Bruggeman 2006; Geremia et al. 2011, 2014b). As snow depth increases, bison move to winter ranges with larger snow-free areas that increase foraging efficiency and allow for greater aggregations of animals (Meagher 1998; Bjornlie and Garrott 2001; Bruggeman et al. 2009b; Fortin et al. 2009).

Large annual differences in the timing, extent, and hardness of snow pack, as well as the emergence of snow-free areas in spring, occur in northern Yellowstone. Consequently, bison are less likely to track changes in food resources at broad scales because they cannot depend on being able to access food in specific seasonal ranges during similar times each year (Geremia et al. 2014b). Higher-elevation areas with more available forage (due to high summer plant growth) and some snow cover may provide increased access to food compared to lower elevation areas with less snow but less available forage (due

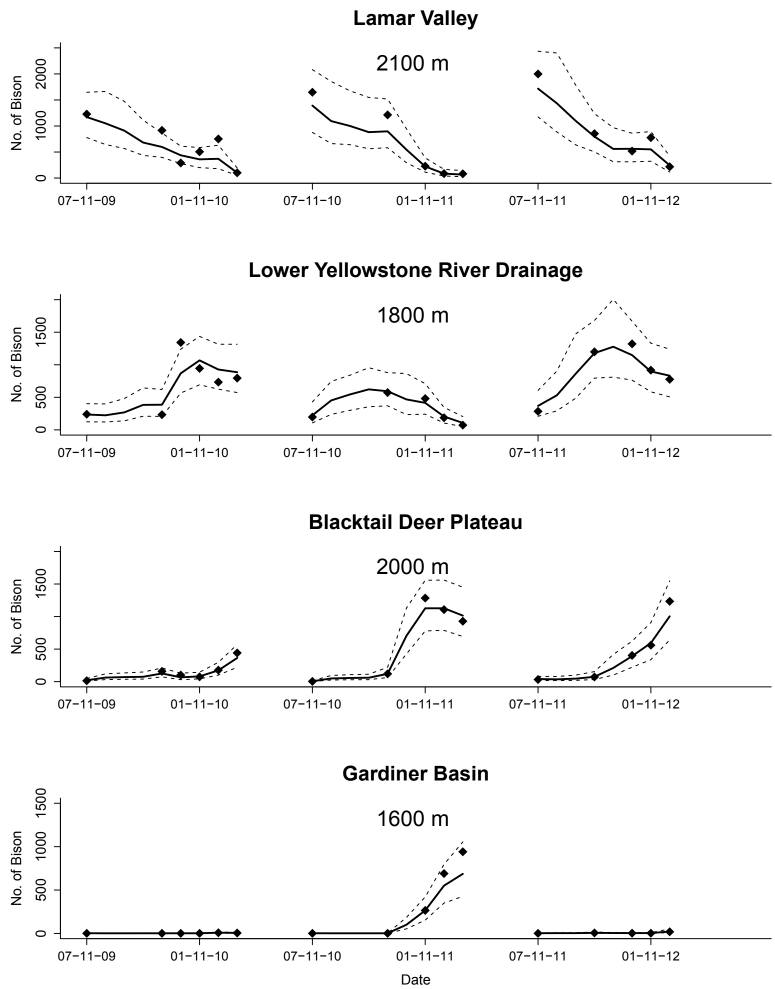


*Figure 4.5. Numbers of bison on winter ranges in the northern region of Yellowstone National Park during 2009 through 2012 (adapted from Geremia et al. 2014b). The Blacktail Deer Plateau and Gardiner Basin are lower-elevation areas and substantial between-year variations exist in numbers of bison moving to these winter ranges. Solid and dashed lines represent medians and 95 percent credible intervals. Date labels on the horizontal axis are numerically formatted as month-day-year.*

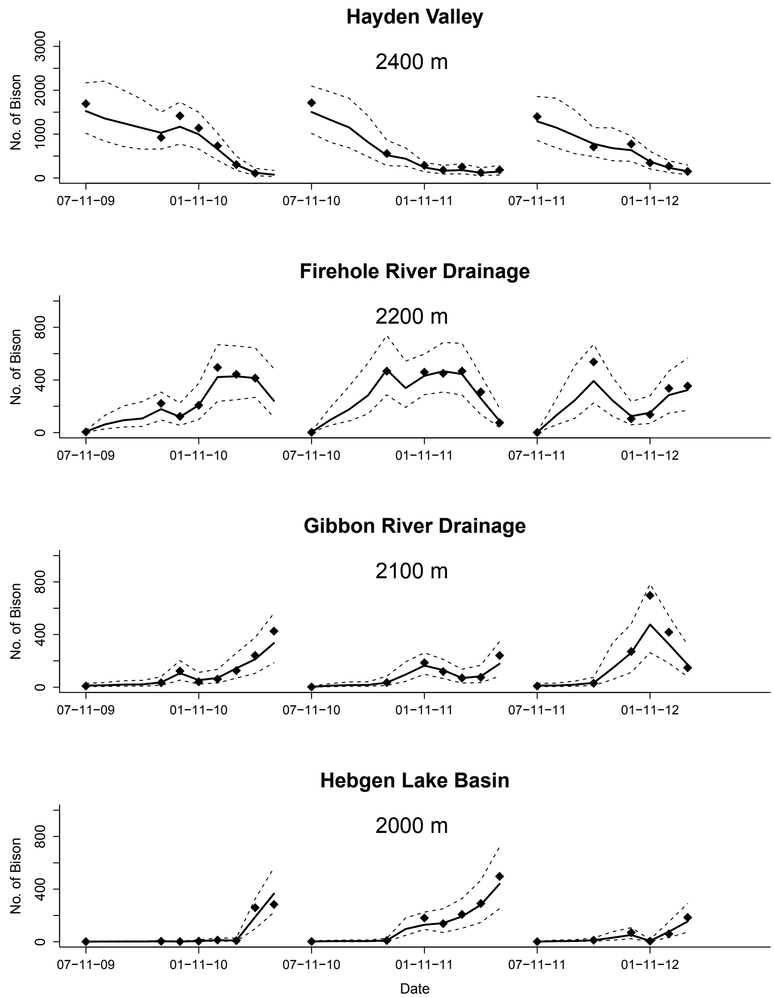


*Figure 4.6. Numbers of bison on winter ranges in the central region of Yellowstone National Park during 2009 through 2012 (adapted from Geremia et al. 2014b). Solid and dashed lines represent medians and 95 percent credible intervals. Date is numerically formatted as month-day-year.*

to lower summer plant growth). However, in years with high snow cover, foraging efficiency in higher-elevation areas decreases and bison must move to lower-elevation areas. Bison learn to respond to these changes in foraging efficiency, and as a result, there are large annual variations in numbers of bison on specific winter ranges (Geremia et al. 2014b; Figure 4.5).

In central Yellowstone, bison exhibit regular seasonal distributions because the timing and extent of snow conditions are similar among years (Figure 4.6). Annual variations in snow pack and melt-out occur, but overall, conditions are similar enough among years to decrease foraging efficiency in a predictable manner. As a result, bison learn to move to specific ranges at specific times of year to exploit differences in food availability (Geremia et al. 2014b). This is most apparent in the Hebgen Lake basin where several hundred bison from central Yellowstone move during April and May to access newly emerging vegetation after snow melt-out (Geremia et al. 2014b).

*Yellowstone bison can move long distances in relatively short periods of time—occasionally traveling more than 30 kilometers (19 miles) in a single day.*

## Conclusions

Large annual migrations of bison to low-elevation winter ranges north and west of Yellowstone National Park highlight the importance of these areas (Plumb et al. 2009; Geremia et al. 2011). Most bison migration into Montana occurs in late February and March across the north boundary, and in April and May across the west boundary, as new grass begins to grow on lower-elevation ranges (Thein et al. 2009; Geremia et al. 2014b). Bison migration back to interior park ranges typically occurs during April through June, following the wave of growing vegetation from lower to higher elevations (Thein et al. 2009; Wilmers et al. 2013).

If migration by bison into Montana is constrained by hazing animals back into the park, then bison numbers will be ultimately determined by food availability within the park. As a result, substantial winter-kill could occur after bison reach high densities (Coughenour 2005; Plumb et al. 2009; White et al. 2013b). To date, the total number of bison in Yellowstone has not reached the estimated food-limited carrying capacity of approximately 5,500 to 7,500 bison during winter (Coughenour 2005; Plumb et al. 2009). However, the population is prolific and still growing despite annual harvests and culling (White et al. 2011). As bison numbers approach or overshoot their food capacity in the park, there could be degradation of vegetation and soils, increased competition with other ungulates, and deterioration of other ecological processes (Coughenour 2005, 2008; Plumb et al. 2009). Alternatively, managers could keep bison at low numbers to reduce the likelihood of large migrations to the park boundary (Geremia et al. 2011, 2014b; White et al. 2013b). Until the late 1970s, there were less than 1,500 bison that generally remained in the park (Meagher 1989b, 1998).

An alternative to constraining bison within Yellowstone National Park or artificially maintaining low numbers is to tolerate bison in nearby areas of Montana, but manage them when they encroach on cattle ranches, highways, and local communities (Treanor et al. 2013; White et al. 2013b). Movements of bison to the northern and western boundary areas of the park are affected by different dynamics, and as a result, require different management prescriptions (Geremia et al. 2014b). Large numbers of bison move across the western park boundary each year and these movements correspond with the calving season when bison are most likely to transmit brucellosis. Thus, space-and-time separation of bison and cattle is needed to reduce the risk of brucellosis transmission, which can be accomplished by fencing livestock and/or moving bison to suitable habitat away from livestock (Treanor et al. 2013; Geremia et al. 2014b).

In contrast, the timing and extent of bison movements across the northern park boundary depend on snow conditions, available forage, and the density of bison in the park (Geremia et al. 2011, 2014b). Large numbers of bison can rapidly move to the northern boundary when conditions severely reduce foraging efficiency, but relatively few bison exit the northern boundary when conditions are mild (Geremia et al. 2011, 2014b). When numbers of bison exceed 1,500 to 2,500 bison in both the central and northern regions of Yellowstone, there is a significant chance that more than one-half will migrate to the northern boundary under severe snow conditions. With similar numbers and average snow conditions, only one-third of the bison are predicted to migrate to the northern boundary; fewer than 200 bison are predicted to move when snow conditions are below average (Geremia et al. 2011, 2014b). If hunting in Montana is used to manage numbers of bison leaving the park, then bison numbers in northern Yellowstone may fluctuate widely over time because few bison are harvested during years when migration is minimal (Geremia et al. 2014b). As a result, it may at times be necessary to capture and remove some bison to meat processing, quarantine, or research facilities to moderate fluctuations in bison numbers (Geremia et al. 2013).


*Bull bison near Obsidian Creek in Yellowstone National Park.*


*Male and female bison in the Lamar Valley of Yellowstone National Park during the midsummer rut.*

# Chapter 5

## REPRODUCTION AND SURVIVAL

*Chris Geremia, P.J. White, Rick L. Wallen, and Douglas W. Blanton*

Reproduction and survival are the key demographic drivers for Yellowstone bison because there is currently no immigration into the population or emigration from the population. As a result, rates of birth and death determine the number of bison. Both of these rates are strongly influenced by human intervention, through the introduction of a nonnative disease (brucellosis) that reduces birth rates and removals of bison due to concerns about the potential for large migrations of bison into Montana and brucellosis transmission to cattle.

### Gestation and Calving

Female bison typically reach sexual maturity and conceive their first calf at 2 or 3 years of age (Meagher 1973; Gogan et al. 2013). Males are capable of breeding at this age, but generally do not until they are 5 or 6 years old because older, larger, and more experienced males monopolize opportunities (McHugh 1958; Berger and Cunningham 1994). The estrus cycle lasts about 3 weeks (19 to 26 days), with females being receptive for one or two days and having one or two ovulations during the breeding season, which mostly occurs from mid-July through mid-August (Meagher 1973; Kirkpatrick et al. 1991, 1993). The gestation period lasts about 285 days (9½ months) and fetal sex ratios appear biased towards slightly more males (Meagher 1973, 1986; Geremia et al. 2014a).[6]

Calves are born during March through June, with the majority of births occurring during late April and May (Jones et al. 2010). Bison give birth to a single calf that weighs between 15 and 30 kilograms (33 to 66 pounds; Meagher 1986). Females often do not separate themselves from other bison when giving birth (Jones et al. 2010). Newborn calves can stand and nurse within 30 minutes, and feed, travel, and rest with groups of adult females and other juvenile animals soon after birth (Meagher 1986). Calves begin eating grass and drinking water within one week, and are usually weaned between 7 and 12 months of age—though some calves have been observed nursing more than 18 months after birth (McHugh 1958; Meagher 1986).

Females can adjust calving by several days to synchronize births and reduce predation risk to most calves through numerical dilution and group defense (Rutberg 1984; Berger 1992; Berger and Cain 1999). However, it is difficult for females in poor body condition to make these adjustments, and as a result, the birthing period is extended following winters with deep snow and later emergence of new vegetation in spring (Berger 1992). Calving dates for bison in northern Yellowstone precede those of bison in central Yellowstone by about 14 days due to the earlier onset of snow melt and new plant growth in northern Yellowstone (Gogan et al. 2005; Figure 5.1). Seventy-two percent (47 of 65) of births in northern Yellowstone occurred by May 7th, while 63 percent (50 of 79) of births in central Yellowstone occurred after May 8th. The calving period in central Yellowstone was prolonged, likely due to harsher winter conditions that predispose female bison to poorer body condition.

Yellowstone bison do not give birth in the same locale each year. Individual radio-collared females have given birth on high-elevation summer areas

6 The data and findings reported in this chapter reflect analyses revised from Geremia et al. 2009 and include data collected during 2009-2014

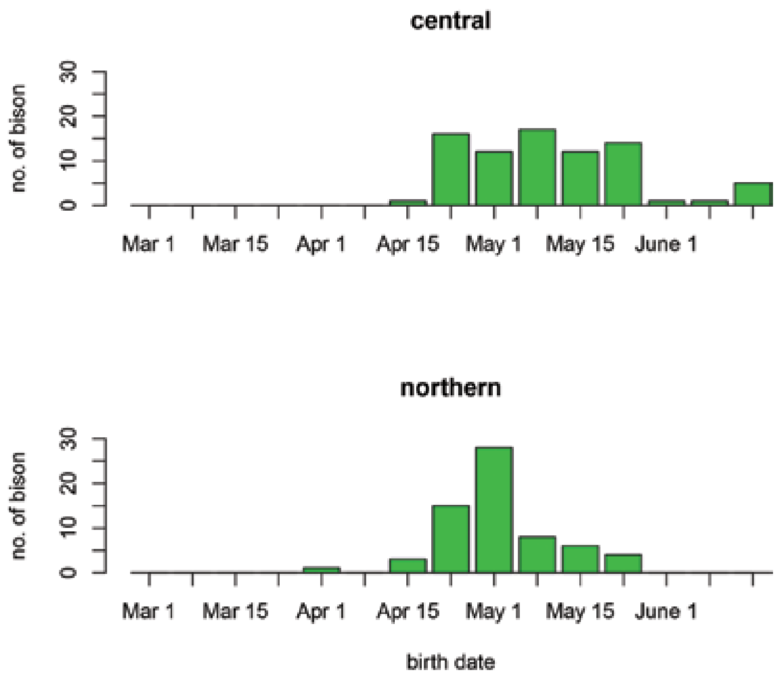


*Figure 5.1. Calving dates of 79 radio-collared bison in central Yellowstone during 2005-2012 and 65 radio-collared bison in the northern region of Yellowstone National Park during 2008-2012 (Geremia et al. 2014a).*

(e.g., Hayden and Lamar valleys) during some years and in lower-elevation winter areas (Hebgen and Gardiner basins) during others. Calving often overlaps with spring migrations from winter to summer ranges, and birth locations likely depend on when these migrations commence—which could be delayed due to prolonged snow pack or late emergence of new vegetation at higher elevations (Geremia et al. 2011, 2014b). As a result, many births occur on winter ranges near or outside the boundary of Yellowstone National Park during some years (Jones et al. 2010).

## Reproductive Rates

After reaching sexual maturity, female plains bison generally produce one calf every one or two years for the rest of their lives (Meagher 1973; Fuller et al. 2007b; Geremia et al. 2009; Gogan et al. 2013). In central Yellowstone, monitored females did not produce calves in sequential years during 1997 to 2003. Rather, most pregnancies were observed in animals greater than 3 years old that were not lactating (Kirkpatrick et al. 1996; Gogan et al. 2013). Lactating bison may not be able to replenish sufficient fat and protein reserves to support pregnancy during summers when drought or competition with other herbivores limit their nutritional intake (Cook et al. 2004a,b, 2013; Gogan et al. 2013; Middleton et al. 2013). However, 54 radio-collared bison monitored between two and nine sequential years during 1997 through 2012 produced a calf more than 60% (136 of 211) of the time, suggesting that bison in central Yellowstone may calve somewhat more frequently than in alternate years. In contrast, sequential calving is more common in northern Yellowstone where 39 radio-collared bison monitored between two and six sequential years produced a calf more than 80% (110 of 132) of the time. Twenty of these females were monitored for at least four consecutive years, with thirteen (60%) producing a calf every year.

In recent decades, birth rates have been higher in northern Yellowstone (0.78; 95 percent Bayesian credible interval [CI] = 0.72 to 0.84) than in central Yellowstone (0.63; CI = 0.56 to 0.69). The probability of giving birth was lowest at 3 years of age and increased with age (Table 5.1; Figure 5.2). A leveling off or decrease of birth rate in older animals has not been detected, which may, in part, be due to limited observations of older animals. In many ungulate populations, birth rates decrease as abundance increases towards the food-limited capacity of the environment to support them (Caughley 1976; Eberhardt 1977, 2002). The number of bison in northern Yellowstone has varied between 400 and 3,500 since 1980, while the number in central Yellowstone has varied between 1,400 and 3,600 bison, with no apparent effects of bison density on birth rates. Instead, population growth has been limited by the capture and shipment of bison to meat processing facilities, and to a lesser extent, hunting in Montana during winter (White et al. 2011). Random variations in weather conditions such as drought or deep snows can limit the availability of forage for bison and increase energetic costs (Clutton-Brock et al. 1985; Sæther 1997; Gaillard et al. 2000). Birth rates for Yellowstone bison were lower following winters with deep or hard snow pack, but no drought-related effects were detected.

| | Reproduction | | Survival | |
|---|---|---|---|---|
| Age | Birthed | Total | Survived | Total |
| 1 | 0 | 0 | 5 | 6 |
| 2 | 0 | 1 | 58 | 58 |
| 3 | 27 | 47 | 64 | 66 |
| 4 | 38 | 53 | 76 | 78 |
| 5 | 43 | 61 | 73 | 77 |
| 6 | 35 | 57 | 63 | 66 |
| 7 | 31 | 44 | 53 | 55 |
| 8 | 28 | 32 | 50 | 52 |
| 9 | 22 | 28 | 49 | 53 |
| 10 | 18 | 24 | 26 | 32 |
| 11 | 13 | 16 | 20 | 24 |
| 12 | 8 | 11 | 13 | 16 |
| 13 | 5 | 7 | 5 | 6 |
| 14 | 3 | 4 | 3 | 4 |
| 15 | 1 | 2 | 4 | 4 |
| 16-20 | 2 | 4 | 7 | 9 |
| **Total** | **274** | **391** | **569** | **606** |

*Table 5.1. One hundred and fifty-three adult female bison were repeatedly monitored between two and nine years for birth and survival during 1996 through 2012 in Yellowstone National Park (Geremia et al. 2014a).*

## Effects of Brucellosis

Some diseases rapidly influence the dynamics of wildlife populations by reducing the survival and fecundity of infected animals (Hudson et al. 1992; McCallum and Dobson 1995). Other diseases establish long-term, endemic infections in populations that persist without a noticeable effect on survival and fecundity (Ewald 1994). Endemic diseases are characterized by a relatively constant proportion of the population being infected, with little variation in the prevalence of

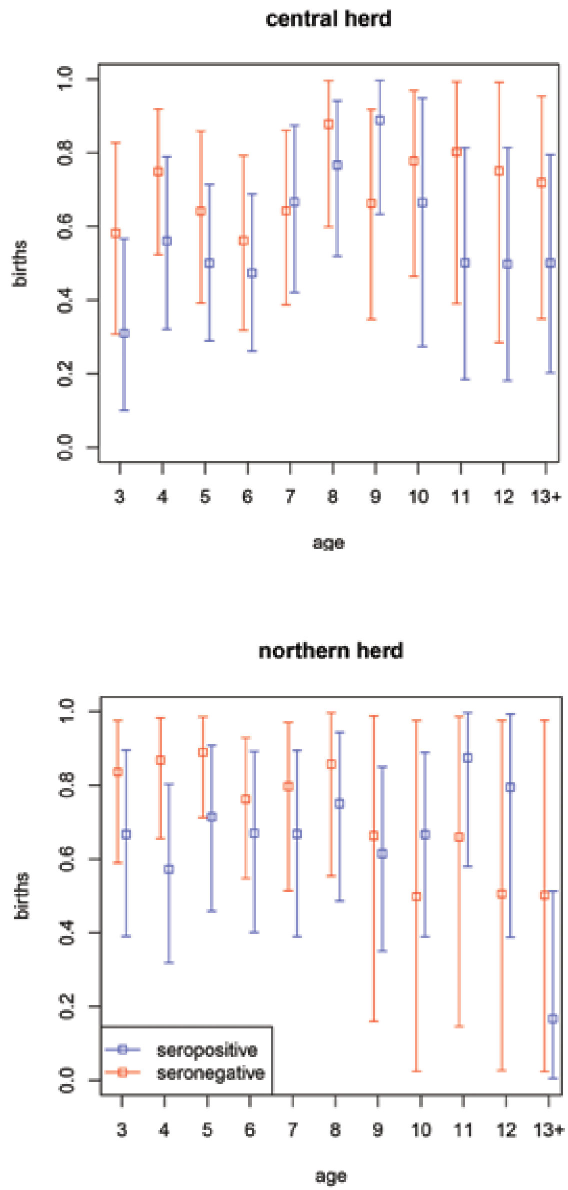


*Figure 5.2. Age-specific probabilities of giving birth for radio-collared bison in the central and northern regions of Yellowstone National Park that were not exposed (red) and chronically exposed (blue) to* Brucella abortus *bacteria (see Chapter 2). Birth probabilities for recently exposed, seroconverting bison are not reported by age but averaged near 0.48.*

infection (Andersen and May 1979). Brucellosis has existed in the Yellowstone bison population for about one century (Meagher and Meyer 1994). The disease does not significantly affect bison survival, but females generally have decreased fecundity during their first pregnancy following infection (Dobson and Meagher 1996; Thorne 2001; Joly and Messier 2005; Rhyan et al. 2009).

The probability of Yellowstone bison giving birth prior to infection with brucellosis was 0.80 (CI = 0.73 to 0.86), but decreased to 0.48 (CI = 0.27 to 0.70) during the first pregnancy after infection (Figure 5.2). However, there was large variability between individuals and about one-half of pregnant bison that were recently exposed to *Brucella* bacteria successfully gave birth to live calves. Many Yellowstone bison are exposed to *Brucella* bacteria prior to reaching reproductive maturity (Treanor et al. 2011). This early exposure may allow immature bison to develop some resistance to infection, thereby reducing the occurrence of *Brucella*-induced abortions when they become reproductively mature (Meyer and Meagher 1997; Geremia et al. 2009).

There is some indication that the probability of Yellowstone bison giving birth to a live calf remains suppressed (0.64, CI = 0.57 to 0.7) for many years following exposure to *Brucella* bacteria due, in part, to lowered pregnancy rates (Figure 5.2). A *Brucella*-induced birth or abortion often results in a retained placenta that could predispose the uterus to infection and cause lower fertility due to delayed ovulation and lower conception rates (Geremia et al. 2009; Rhyan et al. 2009). However, pregnancy rates of females culled at the boundary of Yellowstone National Park during 1997 to 2003 appeared unaffected by brucellosis exposure (Gogan et al. 2013). Likewise, Joly and Messier (2005) did not detect effects of brucellosis exposure on pregnancy rates in wood bison (*Bison bison athabascae*) in Canada. Further research is necessary to resolve these disparate findings.

## Survival

Some female bison live for more than 20 years in Yellowstone (Udevitz and Gogan 2010). Males rarely live past 12 years, perhaps due to higher energetic costs and increased risk of injury when sparring for mates during the breeding season (Meagher 1973). Newborn bison have an increased risk of mortality from predation, disease, and harsh weather. However, their survival has been remarkably high in recent decades, especially compared to other ungulates such as elk (less than 0.3) following the recovery of grizzly bears and wolves (Barber-Meyer et al. 2008; Hamlin et al. 2009). Neonate survival has been 0.75 (standard deviation = 0.06) during the first month of life and 0.87 (standard deviation = 0.05) during the remainder of the first year (Geremia et al. 2014b).

The probability of an adult female bison surviving one year was 0.96 (CI = 0.94 to 0.98) in northern Yellowstone and 0.91 (CI = 0.88 to 0.94) in central Yellowstone during recent decades (Figure 5.3). Survival rates decreased during years with deep snow pack, but remained relatively unchanged through substantial variations in bison abundance and drought conditions. Survival remained consistently high for 3- to 9-year-old females in northern Yellowstone. There was some indication of lower survival rates as females aged past 10 years, but additional data are needed to better define this relationship (Figure 5.3). Lower survival was more prominent in females from central Yellowstone after 9 years of age (Geremia et al. 2009, Figure 5.3). As bison age, tooth wear reduces their ability to chew plant material into small enough particles to facilitate efficient digestion by microbes in their rumen (Van Soest 1994; see Chapter 6). In central Yellowstone this wear may be worsened by the abrasive action of silica present in rhyolite soils, some of which may be retained on plants eaten by bison (Garrott et al. 2009b; Geremia et al. 2009).

## Causes of Mortality

Since 1985, more than 6,000 bison have been removed from the population by humans, primarily through capture and shipment of bison to meat processing facilities and secondarily through hunting (White et al. 2011). Overwhelmingly, these removals have been the principal causes

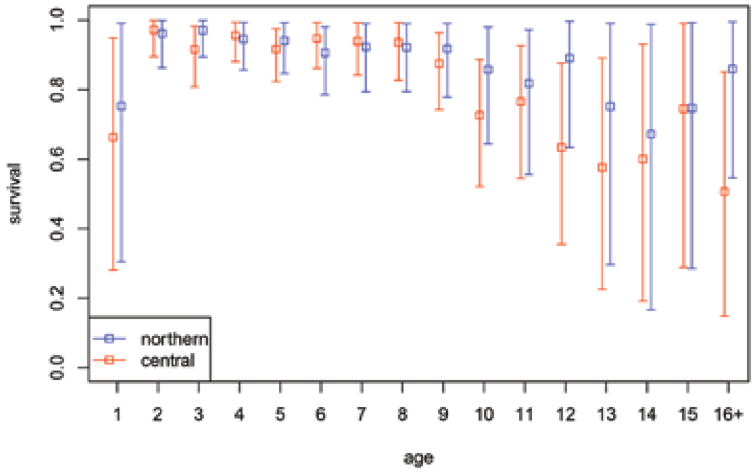


*Figure 5.3. Age-specific probabilities of survival for radio-collared bison in the northern and central regions of Yellowstone National Park. Human removals were not included in the analyses.*

of bison mortality. Winter-kill can be a significant cause of mortality during winters with severe snow pack (Fuller et al. 2007b; Geremia et al. 2009). Also, predation is becoming a larger factor following wolf restoration and grizzly bear recovery (Smith et al. 2004, 2013; Becker et al. 2009a,b). During 1993 through 2010, biologists from Montana State University found 656 bison carcasses in central Yellowstone during winter and spring and the apparent causes of death were 225 wolf predations, 181 winter-kills, 153 due to unknown causes, 46 grizzly bear predations, 20 thermal/mud entrapments, 10 vehicle strikes, 7 accidents/injuries, 7 birth/pregnancy complications, 6 due to unknown predators, and 1 coyote predation (R. A. Garrott, Montana State University, unpublished data).

Wolves in northern Yellowstone primarily feed on elk, with bison comprising only 2 to 6 percent of kills (Metz et al. 2012). Since 1995 when wolves were initially restored, counts of northern Yellowstone elk have decreased from about 19,000 to 4,000 while counts of bison in this region have increased from about 900 to 3,500 (White et al. 2012; see Chapter 1). Despite these changes, wolves have not begun preying

*Infrared image of wolves feeding on a bison carcass in Yellowstone National Park.*


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substantially more on bison, even though wolf numbers in northern Yellowstone decreased from 95 in 2007 to 34 by 2014 due to wolves killing other wolves, malnutrition, and disease (Metz et al. 2012). Bison are larger and employ group defenses that make them more difficult to attack than elk, which are smaller and often run when attacked (Smith et al. 2000; MacNulty et al. 2007; Becker et al. 2009a).

*Some female bison live for more than 20 years in Yellowstone National Park.*

Wolves in central Yellowstone also strongly prefer elk, even though bison are more abundant during winter and elk counts have decreased by about 95 percent since wolf colonization in 1998 (Becker et al. 2009a,b; Garrott et al. 2009a,c). Wolves kill more bison in late winter as snow pack increases and its effects reduce bison condition and increase their susceptibility to attack (Becker et al. 2009a,b). As an example, bison comprised 53 percent wolf diets during 2006 when snow pack was severe, but only 15 percent of wolf diets during the relatively mild winter of 2007 (Becker et al. 2009a,b). Wolves also kill more bison as bison numbers increase relative to elk and there are more bison calves in the population (Becker et al. 2009a,b). The average age of adult bison killed by wolves was 10 years (Becker et al. 2009a,b). Wolves can exist almost entirely on bison, as observed in Wood Buffalo National Park in Canada (Carbyn and Trottier 1987). At this time, however, wolves in Yellowstone still prefer elk and only tend to kill significant numbers of bison during winters with deep and prolonged snow pack that make malnourished animals more abundant and susceptible (Becker et al. 2009a).

## Conclusions

An isolated population of wildlife that adapts to local environmental conditions and reproduces faster than individuals die will generally increase in abundance. Because habitat for many wildlife species is limited in modern society, these types of populations often exhibit boom-and-bust cycles with rapid population growth punctuated by sizeable mortality events (e.g., starvation, culling) when food, other resources, or human tolerance become scarce (Caughley 1970). This is the situation in which Yellowstone bison currently exist because: (1) there is a limited amount of winter range and forage for bison inside Yellowstone National Park, (2) there is limited space in Montana where bison are allowed to migrate and disperse, (3) predation removes relatively few bison, and as a result, has limited effects on population abundance, (4) under-nutrition (starvation) only contributes to high mortality when bison abundance is high and/or snow pack is above average, and (5) most bison migrate to lower elevation areas in response to such severe weather events—which eventually brings them into conflict with agriculture and residential development.

Managers could allow the Yellowstone bison population to continue boom-and-bust cycles, and implement episodic, large removals when population abundance is high (e.g., more than 4,500 animals). These removals would reduce migrations outside of the park for several years as a substantially smaller population again increases in size. Alternatively, managers could attempt to regulate the bison population within a range where enough animals exit the park annually to implement harvests and smaller management removals that offset growth. The target range should be defined by ecological conditions that may vary over time, but under current conditions is near an end-of-winter population of 3,000-4,000 bison (Geremia et al. 2014a). However, this approach necessitates tolerance for bison outside of the park, especially during years when severe winter weather increases numbers of migrating animals.


*Bison grazing among the sagebrush near the Blacktail Deer Plateau in Yellowstone National Park.*

# Chapter 6

## NUTRITIONAL ECOLOGY

*John J. Treanor, Jessica M. Richards, and Dylan R. Schneider*

The availability of an adequate food source is essential for the persistence of any wildlife population. Many species of herbivorous mammals exist in dynamic environments in which the quality of this food source changes seasonally. Yellowstone National Park is one such environment where seasonal fluctuations in environmental conditions have a strong influence on key life events for large herbivores. In such a dynamic landscape, it is expected that individuals maximize their ability to influence the outcomes of these life events by using different strategies within seasons (Barboza et al. 2009). In this chapter, we describe how nutrition influences survival early in life, growth needed to reach reproductive maturity, and successful breeding during adulthood in Yellowstone's bison population, with particular attention paid to how bison use seasonal strategies to meet their nutritional needs.

## Forage Quality, Digestion, and Metabolism

Wild herbivores survive on forage that varies in quality and availability throughout the year (Van Soest 1994). The preferred forage of Yellowstone bison is grasses and sedges, with forbs and shrubs making up less than 6 percent of their diets (Meagher 1973). Shrubs tend to retain a higher nutrient content throughout the growing season, but they also contain a variety of compounds, such as tannins, that limit digestibility (Rhoades 1979; Hanley et al. 1992). For Yellowstone bison, seasonal changes in diet quality reflect the predictable phenology of grasses. The high-elevation ranges in Yellowstone National Park are dominated by cool season grasses that tend to be high in nutrients in the spring, but decrease as the growing season progresses.

The quality of forage is determined by environmental conditions that influence plant growth and the stage of plant maturity (Van Soest et al. 1978; Nelson and Moser 1994). Environmental factors such as precipitation, summer temperatures, and winter severity influence the quality and growth of forage within a given year. During the growing season, younger plants contain more soluble carbohydrates and less fiber, which makes them more digestible than older plants. However, grasses mature quickly and become fibrous, which greatly reduces their digestibility (Rinehart 2008). Thus, it takes more time for bison to extract nutrients from ingested forage as the growing season proceeds.

Bison have a four-chambered stomach that can process bulky amounts of fairly indigestible plant components (Hofmann 1989). The fore stomach, or rumen, serves as a fermentation chamber where millions of bacteria, protozoa, and fungi convert cellulose into energy-yielding fatty acids that are digestible by bison (Owen-Smith 2002). Dietary energy provides the nutrients for growth, heat production, and the maintenance of body functions primarily through the metabolism of glucose (Rinehart 2008; Barboza et al. 2009). The protein content in forage provides rumen microbes with essential amino acids for the synthesis of microbial proteins. These proteins are absorbed by bison as they pass through the rumen and then used for the development of body tissues and other vital functions. In other words, energy is supplied to bison through the fermentation of dietary carbohydrates, while protein is supplied through the digestion of rumen microbes (Van Soest 1994).

Gut capacity increases with body size in ruminants, which allows larger animals to eat a diet high in fiber and retain and ferment forage longer (Demment and Van Soest 1985; Gordon and Illius 1996; Larter and Nagy 2001). The amount of fibrous forage in bison diets increases during winter when plant tissues are dead. As a result, forage is retained longer in the gut because indigestible plant tissues must be reduced in size to pass through the openings in the rumen. Bison also ruminate, whereby food is returned to the mouth from the gut for intensive chewing to further break down plant material. The frequency and duration of rumination bouts increase as diets become more fibrous (Renecker and Hudson 1993; Sinclair et al. 2006). The ruminant digestive system is not designed to maximize the flow of ingested forage (Hume 1989). As a result, seasonal changes in the digestibility of forage plants correspond to a reduction in foraging time and the rate of forage intake (Spalinger et al. 1986; Owen-Smith 2002). Small reductions in the quality of winter diets have been associated with large declines in food intake, which demonstrates that bison cannot compensate for low quality forage by simply eating more (Gray and Servello 1995; Cook et al. 2004a).

In general, bison have peak forage intake and maintenance requirements during June through September (Rutley and Hudson 2000). However, low temperatures and snow cover during winter creates high energy demands at a time when less energy is available in forage plants (Sinclair et al. 2006). Bison adjust by reducing food intake and metabolism and decreasing their energy expenditures (Christopherson et al. 1979; Stuth 1993; Galbraith et al. 1998; Feist 2000; Signer et al. 2011). North American bison have adapted to survive winter conditions when food is limited. Bison generate heat through digestive fermentation, especially from the high roughage diets that are available during winter (Owen-Smith 2002). Body heat is then conserved by a layer of subcutaneous fat underneath a thick winter coat. In comparison, bison are more tolerant of cold temperatures than cattle, with 6-month old bison calves being as tolerant of cold as yearling cattle (Christopherson and Hudson 1978; Christopherson et al. 1979). Bison have developed an effective strategy for meeting the nutritional demands of survival, growth, and reproduction across seasons by selecting forage for high nutritional value from spring to autumn and minimizing nutritional needs and the loss of body reserves during winter (Barboza et al. 2009; Stephenson et al. 2002).

## Seasonal Nutrition and Population Dynamics

*The availability of high quality food during lactation and the early years of life could also influence the social status and lifetime reproductive success of Yellowstone bison.*

High quality diets are important during calf development because protein requirements increase, particularly in late winter and early spring when the fetus grows rapidly (Robbins and Robbins 1979; Robbins 1993; Cook 2002). In Yellowstone, the protein content of forage is lowest during late winter and early spring, which coincides with the high nutritional demands of late gestation (Treanor 2012). The survival of newborn calves is reduced by low maternal diet quality, especially if food is restricted for extended periods near parturition (Price and White 1985; Barboza et al. 2009; Cook et al. 2013). Pregnant bison mobilize fat and protein body reserves during late gestation to meet increasing nutritional demands (Treanor 2012). As a result, female bison lose a substantial amount of body mass over winter, especially if winters are severe and prolonged.

In spring, bison give birth to a single calf which must travel with the herd soon after birth (Renecker and Hudson 1993). Newborn calves require milk of high nutritional quality to grow quickly. Thus, lactation is the most nutritionally demanding stage of reproduction in mammals, with protein requirements increasing 110 to 130 percent (Oftedal 1985; Barboza and Parker 2008; Barboza et al. 2009). However, the onset of lactation for bison frequently occurs when deep snow still impedes plant emergence and access to high-elevation rangelands within Yellowstone National Park. Access to emerging forage is critical for the development of newborns because milk fat is primarily derived from the daily diet rather than body reserves (Sadleir 1987; Pond et al. 2005). Milk production reaches a peak several weeks after parturition and gradually declines thereafter (Renecker and Hudson 1993). Thus, the growth rate of bison calves and their body size entering winter reflects the food available to their mothers for milk production.

Lactating females need to replenish body reserves that were depleted the previous winter and spring to become pregnant in late summer (Cook et al. 2001). Ovulation in bison is influenced by the nutritional condition of females and their access to summer forage with adequate digestible energy (Schillo 1992; Gerhart et al. 1997; Cook et al. 2013). Therefore, the accumulation of body fat through summer and autumn nutrition plays an important role in reproductive success (Clutton-Brock et al. 1997; Russell et al. 1998; Cook 2002). After the metabolic needs of bison are met by dietary nutrients, excess energy and protein are deposited in the form of fat and muscle. Fat is typically stored towards the end of summer because subcutaneous fat can limit the exchange of heat with the environment (Owen-Smith 2002; Barboza et al. 2009).

The availability of high quality food during lactation and the early years of life could also influence the social status and lifetime reproductive success of Yellowstone bison. Body mass is a reliable indicator of female body condition and significantly correlated with dominance rank in bison (Lott and Galland 1987; Green and Rothstein 1991; Vervaecke et al. 2005). A higher rank may improve feeding opportunities, especially during periods of food restriction. Also, the maternal rank of bison is positively related to offspring weight (Vervaecke et al. 2005). Bison that are small at birth or grow more slowly because of inadequate nutrition may become small adults and produce fewer offspring over their lifetimes (Gaillard et al. 2003; Barboza et al. 2009).

Reproduction has a cost that is mostly evident in animals in poor nutritional condition (Festa-Bianchet et al. 1998). As a result, nutritional condition can interact with bison density to influence the productivity of the population. For example, conception rates are lower in populations at high density, which reduces mortality risk to reproductively mature females in poor condition (Gaillard et al. 2000). Furthermore, nutritional effects are subtle and influence many different aspects of reproduction and survival. In combination, these effects may result in substantial limitations on population growth (Cook et al. 2013).

NPS/Neal Herbert

*Bison feeding near Lower Geyser Basin in the west-central portion of Yellowstone National Park.*

## Seasonal Strategies

Yellowstone bison have responded to seasonal changes in forage availability and quality by overlapping the most nutritionally demanding phases of their life cycle with the availability of high quality forage (Rutberg 1984; Post et al. 2003; Treanor 2012). About 80 percent of their calving occurs during April 25 through May 25, which coincides with the emergence of growing forage on low-elevation winter ranges (Jones et al. 2010; Treanor 2012). Thus, lactation commences when forage high in protein and digestible energy becomes available (Figure 6.1). The availability of high-quality vegetation after birth increases the quality of milk and provides an advantage for early born juveniles (Guinness et al. 1978; Festa-Bianchet 1988). Over-winter mortality is typically lower for larger juveniles as a result of better body condition (Clutton-Brock et al. 1982; Festa-Bianchet 1988; Keech et al. 2000; Côté and Festa-Bianchet 2001). Therefore, timing the birth of calves with emerging vegetation is an effective strategy for maximizing the growth of newborns in the early months of life, which increases their ability to survive the upcoming winter.

In addition, Yellowstone bison adjust their nutritional intake through habitat selection and migratory movements as the availability and quality of forage changes seasonally across the landscape. They move from summer ranges at relatively high elevations to lower elevations during autumn through winter, and then return to the summer ranges in June (Meagher 1989b; Bjornlie and Garrott 2001; Bruggeman et al. 2009c). Vegetation quality has little influence on the selection of foraging areas used by bison during winter because plant tissues have senesced and are of low nutritional value. Instead, factors that influence the availability of forage such as snow pack and bison density become more important (Bruggeman 2006). As a result, most bison move to foraging areas at lower elevations and areas with thermally warmed ground as snow depths increase at higher elevations (Meagher 1989b; Bruggeman et al. 2009c).

During spring, there are more energy-efficient foraging opportunities for bison at lower elevations because snow melt and vegetation growth commence earlier (Despain 1990; Thein et al. 2009). Thus, most calving occurs in these areas (Jones et al. 2010). The return migration of bison

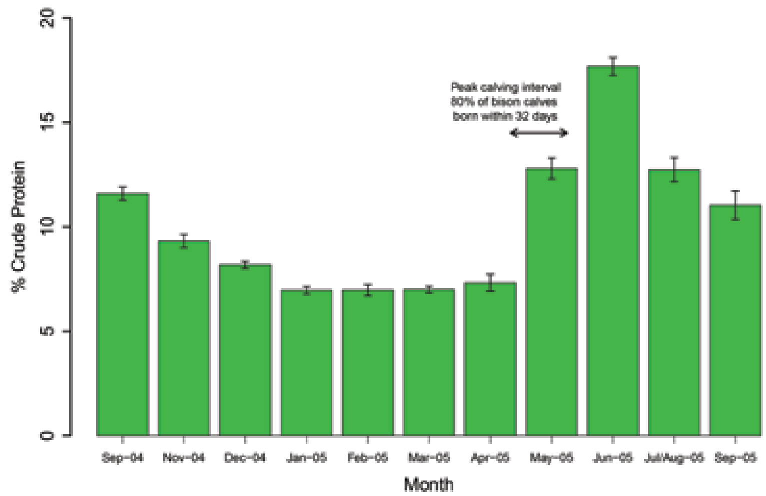


*Figure 6.1. Monthly percentage (mean ± standard error) of fecal crude protein from Yellowstone bison sampled during 2004 and 2005. The peak calving interval was reported in Jones et al. (2010). Bison calving is synchronized with the emergence of spring vegetation, which is high in protein and digestible energy. Sep-04 refers to September 2004.*

to higher-elevation summer ranges coincides with patterns of new vegetation growth on the landscape (see Thein et al. 2009 for detailed descriptions and maps). Highly digestible plants eventually become widely distributed, and as a result, energy intake by bison increases (Mysterud et al. 2001). As the growing season advances and grasses mature there is a decrease in the proportion of higher-quality leaves to lower-quality stems (Ball et al. 2001). As a result, bison become more selective and consume the upper portions of grasses which are higher in crude protein and digestible energy (Rutley and Hudson 2001).

## Conclusions

Yellowstone bison have developed a set of strategies to meet their nutritional needs across the year. The availability of high quality forage during spring and summer promotes successful reproduction and the accumulation of body reserves for winter survival, while winter forage helps reduce the rate at which these reserves are mobilized. As winter progresses, fat reserves may be needed for energy, especially for pregnant females during late gestation. Calving is synchronized with the emergence of spring forage, which allows bison to meet the high nutritional demands of lactation. The growth and survival of calves is positively affected by the nutritional quality of summer forage. Therefore, bison increase forage intake during the growing season, which enhances assimilation of nutrients. During the dormant season, food intake is reduced and bison conserve body reserves by reducing activity and metabolic rates. Lower-elevation winter ranges provide bison with access to forage and reduce the energy expenditure of moving through the deep snow found at higher elevations. Yellowstone bison are adapted to seasonal changes in forage nutrition and winter conditions with digestive, physiologic, and behavioral strategies that allow them to survive and reproduce in a dynamic environment.


*Bison and cowbirds during the spring green-up in Yellowstone National Park.*

# Chapter 7

## ECOLOGICAL ROLE—BISON RELATIONS WITH OTHER ANIMALS AND EFFECTS ON GRASSLAND PROCESSES

*Rick L. Wallen, P.J. White, and Chris Geremia*

Populations of large grazers like bison have strong influences on plant and animal communities (Knapp et al. 1999; Lott 2002; Bailey 2013). Grazing often increases the availability and distribution of nitrogen to plants, which in turn, can increase plant production (Frank and McNaughton 1993). Also, bison provide food for many predators, scavengers, and decomposers, and their carcasses deposit nutrients into the soil that create fertile patches for plant growth (Knapp et al. 1999). In addition, grazing and wallowing create specific environments that result in greater plant diversity across the landscape by holding water in depressions, enabling colonization by pioneering plant species, and increasing the diversity and use of areas by other animals (Knapp et al. 1999; Truett et al. 2001; Fuhlendorf et al. 2006).

## Ecosystem Engineers

Bison inadvertently act as "ecosystem engineers" by creating and responding to heterogeneity across the landscape (Gates et al. 2010). They create greater plant diversity by preferentially feeding on grasses and avoiding some flowering plants, while preventing plant community succession through hoof action and horning or rubbing on trees and shrubs (Meagher 1973; Coppedge and Shaw 1998; Knapp et al. 1999). Their heavy bodies and sharp hooves combine to till the soil and disturb roots of grasses and grass-like plants (Frisina and Mariani 1995). This prevents grassland succession to shrubs or trees and provides grasses with greater access to sunlight, which is important for growth (Knapp et al. 1999). Large groups of bison contribute to natural disturbances that influence plant species composition and distribution across large portions of grasslands and shrub steppe, similar to fire, windthrow, and mass soil erosion events (Augustine and McNaughton 1998; Turner et al. 2003; Collins and Smith 2006; McWethy et al. 2013). Fire can increase grassland productivity through nitrogen cycling, but tends to reduce the diversity of plant species because not all species are fire tolerant. Grazing by bison is more likely to retain a diversity of plant species while redistributing nitrogen in the system (Knapp et al. 1999; Frank et al. 2000). Moderate grazing induces the production of new grass tissue and increases plant community production to the limits determined by water and nitrogen availability (McNaughton 1983, 1984; Frank et al. 2013). Fire tends to burn fewer plants in grazed areas because ungrazed grasses contain more flammable material. Thus, the combined effects of grazing and fire—called pyric herbivory—can result in greater plant diversity and habitat heterogeneity than either process alone (Fuhlendorf and Engle 2004; Fuhlendorf et al. 2008, 2012).

## Food-Limited Carrying Capacity

Bison eat frequently due to their large body size, which combined with their tendency to aggregate into herds, necessitates finding food sources that are abundant or widely distributed. As a result, bison often congregate in large open grasslands for breeding, but then disband into smaller


*Bison wallowing in the Lamar Valley of Yellowstone National Park.*

groups and disperse widely on smaller patches of habitat through the rest of the year (Berger and Cunningham 1994). The influence of bison grazing on plant communities can be intense at times due to their grouping tendencies, but they rarely occupy the same foraging area for more than a few days (McHugh 1972; Knapp et al. 1999). Bison select areas with plants high in nutrients during the growing season, but transition to areas with relatively high plant abundance and availability during winter when grasses are past their growing period and there is relatively little variation in quality among areas (Wallace et al. 1995). Bison can move more than 46 centimeters (18 inches) of snow by swinging their massive heads in a side-to-side motion, which allows them to access the aged vegetation beneath and feed in areas where other ungulates cannot during winter (Barmore 2003; Picton 2005).

*Grazing and wallowing create environments that result in greater plant diversity across the landscape.*

Grasses and grass-like plants are important foods for several ungulates in Yellowstone National Park, including bison (97 to 99 percent of diet in winter), elk (81 to 86 percent), and bighorn sheep (*Ovis canadensis*; 61 to 67 percent; Singer and Norland 1994). As bison numbers in northern Yellowstone increased during the 1970s and 1980s, they expanded their geographic range and began using more sedge meadows, grasslands, and sagebrush areas (Jerde et al. 2001). As a result, their diet and habitat overlap with other ungulates increased, including a moderate overlap in diet and a large overlap in habitat with elk that could contribute to competition between them for food and space (Singer and Norland 1994; Coughenour 2005; Plumb et al. 2009). In turn, some people questioned whether bison had surpassed numbers that could be supported by the forage in the park and nearby areas, considering year-to-year variations in food production, habitat use, diet selection, competition, and energy use.

Dr. Michael Coughenour of the Natural Resource Ecology Laboratory at Colorado State University evaluated if bison had reached a food-limited carrying capacity by developing and testing a model of the Yellowstone system that incorporated abiotic variables (e.g., soil nutrients, water, topography, weather) and biotic processes (e.g., plant growth, herbivory, predation, and the abundance, distribution, energy balance, and nutrition of bison and elk). Model output indicated the food-limited carrying capacity for bison in and near Yellowstone National Park was as large as 10,000 bison during summer but varied around 6,500 during winter, near which foraging efficiency and bison condition should decrease (Coughenour 2005; Plumb et al. 2009). To date, bison numbers have not reached this level, and several assessments of vegetation conditions by scientists and land managers have indicated the park is not overgrazed (Boyce 1998; Huff and Varley 1999; National Research Council 2002).

However, model output also predicted a substantial decrease in the number of elk in northern Yellowstone could release bison in this area from competition and induce an increase in their numbers to as many as 4,900 (Coughenour 2005; Plumb et al. 2009). This forecast was supported as counts of northern Yellowstone elk decreased from about 19,000 in 1994 to 4,000 by 2013 following wolf restoration and grizzly bear recovery, while bison numbers increased from approximately 870 to 3,500 (Frank et al. 2013; Garrott et al. 2013). The specific causes of these coinciding trends remain unknown, but the number of bison in northern Yellowstone is still increasing despite occasional culling, with high calf production and survival of all age groups (Table 7.1). Bison will likely respond to increased competition and nutritional stress as their numbers increase by moving to lower elevation winter ranges outside the park in search of food (Coughenour 2005). This behavior is consistent with large migrations of bison outside the park during severe winters in the past decade (Coughenour 2005; Plumb et al. 2009). Scientists are studying the effects of this change from an elk- to a bison-dominated system on the ungulates and vegetation in northern Yellowstone (Hebblewhite and Smith 2010; Garrott et al. 2013).

## Effects of Grazing

Bison can enhance plant growth by making nitrogen and organic matter more abundant and accessible to soil microbes, and distributing nutrients across the landscape (Frank and Evans 1997; Towne 2000; Augustine and Frank 2001). During the 1980s and 1990s, the grazing of

| Growth rate | | |
|---|---|---|
| | Average | 95% range |
| 2000-01 | 1.20 | 1.12 – 1.27 |
| 2001-02 | 1.20 | 1.13 – 1.26 |
| 2002-03 | 0.94 | 0.88 – 1.01 |
| 2003-04 | 1.10 | 1.03 – 1.16 |
| 2004-05 | 1.17 | 1.10 – 1.24 |
| 2005-06 | 0.75 | 0.69 – 0.81 |
| 2006-07 | 1.18 | 1.12 – 1.25 |
| 2007-08 | 0.55 | 0.48 – 0.61 |
| 2008-09 | 1.10 | 1.04 – 1.17 |
| 2009-10 | 1.17 | 1.10 – 1.23 |
| 2010-11 | 0.96 | 0.89 – 1.02 |
| 2011-12 | 1.12 | 1.06 – 1.19 |
| 2012-13 | 1.15 | 1.09 – 1.22 |
| 2013-14 | 0.99 | 0.92 – 1.05 |

| Vital rates | | |
|---|---|---|
| | Average | Standard deviation |
| Adult female survival | 0.93 | 0.01 |
| Neonate survival (1st month) | 0.75 | 0.06 |
| Calf survival (rest of 1st year) | 0.87 | 0.05 |
| Male survival | 0.94 | 0.04 |
| Probability of newborn calf being female | 0.47 | 0.02 |
| Birth rate | 0.70 | 0.03 |

*Table 7.1. Population growth rate (including winter removals) and vital rates of Yellowstone bison during the Interagency Bison Management Plan (Geremia et al. 2014b).*

grasses and deposition of organic matter by migratory ungulates (primarily elk) in northern Yellowstone approximately doubled the rate of nitrogen mineralization and production of leaves, roots, and stems by grasses (Frank and McNaughton 1993; Frank and Groffman 1998; Frank et al. 2002). However, rates of ungulate grazing and nitrogen cycling decreased by up to one-half during the late 1990s as the numbers of elk decreased substantially due to hunter harvest, predation, and winter-kill (Frank 2008). Also, energy and nutrient dynamics were rearranged across the landscape, with grazing decreasing more in areas with higher productivity (Frank 2008). Since that time, the number of bison in northern Yellowstone has more than tripled, which could reestablish the stimulating effects of grazing on nitrogen cycling and plant production (Frank et al. 2013). However, large groups of bison that repeatedly graze areas and remove plant tissue through the summer growing season could have quite different effects on Yellowstone's grasslands than herds of elk that graze areas for relatively short periods during their migration to higher-elevation summer ranges (Wallace et al. 1995). Scientists are currently studying the effects of this recent change.

Ungulate grazing and nutrient deposition generally increases grass production from low to moderate grazing intensities, but decreases production at higher grazing intensities because too much leaf tissue is removed (Kie et al. 2003; Stewart et al. 2006). During 1998 to 2000, less than 50 percent of the herbaceous vegetation in the Hayden Valley of central Yellowstone was consumed by herbivores during the growing season, which approximates a moderate grazing rate (Olenicki and Irby 2003). In some areas, however, bison removed more than 30 percent of new growth in spring and 70 percent of the remaining plants during winter (Olenicki and Irby 2003). Higher consumption could decrease plant production if bison numbers continue to increase and bison regraze the same plants during a single season or consecutive seasons (Olenicki and Irby 2003). As a result, the prevalence of grasses could decrease while forbs and grazing-tolerant plants increase—though the outcome will depend on the density of bison relative to the capacity of the environment to support them (Kie et al. 2003; Stewart et al. 2006).

## Apparent Competition

If the current trend of increasing bison numbers and decreasing elk numbers continues, then wolves may begin to rely more on bison for sustenance; which could have indirect effects on elk and other ungulates (Garrott et al. 2009a, 2013; Hebblewhite and Smith 2010). Predation on a particular species can be strongly influenced by the presence of other prey species that maintain predators at higher densities—a process known as apparent competition (Holt and Lawton 1994). For example, an increase in the abundance of one prey species can result in a decrease in the abundance of another prey species due to an increase in the number or distribution of predators (Holt 1977). This situation was observed in the Canadian Rocky Mountains where wolves primarily fed on moose (*Alces alces*), but also killed woodland caribou (*Rangifer tarandus caribou*) as alternate prey. An increase in moose numbers resulted in more wolves that contributed to a range-wide decrease in numbers of less abundant caribou (Wittmer et al. 2005). Garrott et al. (2009a) suggested that increased predation on abundant bison by wolves in the Madison headwaters area of central Yellowstone would also enable them to keep killing more of their primary prey, elk. In other words, abundant bison could sustain wolf hunting in the area despite the scarcity of their preferred prey (Garrott et al. 2013). In turn, wolves could keep the number of elk in the area low by occasionally killing vulnerable animals, as annual counts suggest is currently happening (Garrott et al. 2013).

Elk populations in northern and west-central Yellowstone were near the capacity of the environment to support them for several decades prior to the restoration of wolves (Taper and Gogan 2002; Garrott et al. 2009c; White and Garrott 2013). Elk numbers decreased about 75 percent following wolf restoration due to predation and other factors (White and Garrott 2005; Garrott et al. 2009c; White and Garrott 2013). It is uncertain if predation will ultimately regulate these elk populations at a lower, alternate state or whether bison will become a significant alternate prey for wolves (Garrott et al. 2009a, 2013). Bison are now more abundant than elk in Yellowstone during winter, and wolf use of


*A bald eagle and ravens feeding on a bison carcass in Yellowstone National Park.*


*Bison in the Lamar Valley of Yellowstone National Park.*

bison has increased in recent years (White and Garrott 2013). However, wolves still strongly prefer elk despite their decreased availability (Becker et al. 2009a; Metz et al. 2012). Bison are much more formidable prey for wolves than elk because of their larger size and tendency to employ group defenses whereby adults coalesce around and protect younger, more-vulnerable animals (MacNulty et al. 2007; Becker et al. 2009a). As a result, predation on bison is not currently sustaining more wolves in Yellowstone which could contribute significantly to further decreases in elk abundance (Garrott et al. 2013; White and Garrott 2013). However, scientists are continuing to evaluate the role of bison as an alternate prey because wolves may begin to kill more bison if elk numbers decrease further (Carbyn and Trottier 1987; Hebblewhite and Smith 2010; Garrott et al. 2013).

## Conclusions

The role bison historically served in grassland ecosystems disappeared as society killed them to near extinction and usurped most of their habitat for agricultural, recreational, and residential development (Lott 2002; Franke 2005; Freese et al. 2007; Bailey 2013). While there are now more than 400,000 bison in private and commercial herds used for meat production, the number of bison in conservation herds (less than 20,000) has not increased substantially since the 1930s (Freese et al. 2007). Thus, while the physical form of bison remains throughout the Great Plains, most of these animals provide reduced ecological functions on a much smaller spatial scale (Plumb and Dodd 1993; Lott 2002; White and Wallen 2012; Bailey 2013; Kohl et al. 2013). As a result, wild land preserves like national parks and wilderness areas will continue to provide the core conservation areas where wild bison fulfill the ecological role their ancestors played in shaping the species we see today (White and Wallen 2012). However, we are also encouraged that public land agencies, non-governmental organizations, American Indian tribes, and private landowners are working to build on this core by establishing or expanding wild, wide-ranging populations of bison in several areas where conflicts with humans can be minimized across large landscapes.


*Bison moving snow with its head to feed.*

# Chapter 8

## ADAPTIVE CAPABILITIES AND GENETICS

*Rick L. Wallen and P.J. White*

Today, thousands of Yellowstone bison move across a large landscape and are exposed to natural selection factors such as competition, predation, and severe environmental conditions (Darwin 1859; Plumb et al. 2009). However, this population was nearly extirpated by humans in the late 1800s and culled periodically during the last century (Cahalane 1944; Meagher 1973; White et al. 2011). As a result, there are concerns about the genetic integrity of the population (Halbert et al. 2012). In this chapter, we describe the existing genetic diversity in Yellowstone bison and discuss its preservation to ensure descendants have the ability to adapt to a changing environment.

### Near Eradication

Yellowstone bison experienced a population bottleneck in the late 1800s due to human exploitation (Plumb and Sucec 2006). There were less than 25 indigenous bison in Yellowstone National Park by 1902, all in the central region of the park (Pelican Valley). This population persisted at relatively low numbers (less than 500 bison) for many decades (Meagher 1973). A population that is reduced to a small number of animals contains less genetic variation than the original, larger population—known as the founder effect (Allendorf and Luikart 2007). Thereafter, chance losses of genetic variation may continue due to inadequate gene flow with other populations. Over time, these losses can reduce the abilities of animals to adapt to new environmental challenges (Allendorf and Luikart 2007).

Fortunately, Yellowstone bison do not show the effects of inbreeding and they have retained significant amounts of genetic variation as measured by heterozygosity and allelic diversity (Allendorf and Luikart 2007; Halbert et al. 2012; Wallen et al. 2013). This high genetic diversity despite near extirpation may be due to the restoration of a new herd in northern Yellowstone during 1902 from unrelated bison that eventually interbred with the indigenous bison in central Yellowstone (Dratch and Gogan 2010; White and Wallen 2012). The unrelated bison came from the Pablo-Allard herd (18 females) in northwestern Montana and the Goodnight herd (3 bulls) in Texas (Cahalane 1944; Meagher 1973).

The remnant, indigenous bison in central Yellowstone were once thought to be mountain bison or wood bison (Meagher 1973). However, Wilson and Strobeck (1999) concluded these bison were plains bison based on genetic differences with other populations (also see Franke 2005). Today, Yellowstone bison contribute an important genetic lineage to plains bison that is not found elsewhere, except in populations started with bison relocated from Yellowstone National Park (Halbert and Derr 2008). Yellowstone bison have high genetic diversity compared to many other populations of plains bison, and are one of only a few bison populations with no evidence of interbreeding with cattle (Halbert 2003; Halbert and Derr 2007). However, the population remains isolated because bison rarely move between Yellowstone National Park and the Jackson population in Grand Teton National Park and the National Elk Refuge—even though there are no barriers to such movements.


*Bull bison near Yellowstone's Lamar Valley.*

NPS/Neal Herbert

*Bison scratching on wayside display in Yellowstone's Hayden Valley.*

## Population Subdivision

Yellowstone bison congregate in two primary areas for breeding; the Hayden and Pelican valleys in the central region of the park, and the Lamar Valley and adjacent plateaus in the north (Olexa and Gogan 2007; Halbert et al. 2012). Analyses of mitochondrial DNA have revealed a minimum of two haplotypes in Yellowstone bison (Ward et al. 1999; Gardipee 2007). Haplotype 6 was found in 88 of 94 (94 percent) bison sampled from central Yellowstone and 29 of 57 (51 percent) bison from northern Yellowstone. Haplotype 8 was found in 6 of 94 (6 percent) bison from central Yellowstone and 28 of 57 (49 percent) bison from northern Yellowstone (Gardipee 2007; Wallen et al. 2013). Bison with haplotype 6 carry a double mutation that affects two genes: Cytochrome b and ATP6 (Pringle 2011). This mutation is inherited and could reduce aerobic capacity by affecting the production and transport of energy within cells (Pringle 2011). However, no symptoms have been observed in Yellowstone bison, which have high birth and survival rates despite living in a predator-rich environment with severe winter conditions (see Chapter 5). Thus, it is unlikely this mutation is being expressed and causing metabolic deficiencies. Alternatively, there are often multiple pathways in biological systems that alleviate or circumvent potential metabolic deficiencies. Regardless, the National Park Service is collaborating with Dr. James Derr of Texas A&M University to determine the diversity of mitochondrial DNA haplotypes in the population and evaluate the consequences of mutations that could lead to mitochondrial diseases.

Bison that live in the central and northern regions of Yellowstone have significantly different distributions of alleles and genotypes, and are genetically distinguishable based on 20 alleles only found in one of the two regions (14 central; 6 northern; Halbert et al. 2012). This substructure was likely created and sustained by several events, including: (1) the population bottleneck caused by nearly extirpating Yellowstone bison in the late 19th century, (2) the creation of another breeding herd in northern Yellowstone from bison of unrelated breeding ancestry, and (3) human management thereafter (Meagher 1973;

White and Wallen 2012). Analyses of mitochondrial DNA suggest these regional genetic differences have been maintained by strong female philopatry to breeding areas, with most females returning to the same area each year (Gardipee 2007; Wallen et al. 2013). Also, analyses of microsatellite DNA suggest there were only about two emigrants per decade between the two regions during the 20th century (Halbert et al. 2012).

In the past decade, there has been substantial dispersal of bison between central and northern Yellowstone and subsequent gene flow could lessen these regional genetic differences (White and Wallen 2012). Since 2007, 22 of 114 radio-collared, female bison have emigrated from central Yellowstone to the northern region, or vice versa, and remained through one or more breeding seasons (White and Wallen 2012; Wallen et al. 2013). Each of these females could represent more than one dispersing individual because bison tend to move through the ecosystem in groups of 20 or more (USDI, NPS 2010). Monitoring data supports that 18 of these 22 radio collared females got pregnant on the destination range and produced 44 offspring over several years. In addition, at least 6 of these females brought calves to their destination range that were conceived on their range of origin (White and Wallen 2012; Wallen et al. 2013 updated). Many of these calves likely survived to reproductive age given the high survival of Yellowstone calves through their first year (0.65) and thereafter as adults (0.93; see Chapter 5 and Table 7.1). These observations of female emigration and subsequent reproduction on a new breeding range support estimates of 10 to 20 genetic migrants per decade based on recent sampling of microsatellite genotypes (Wallen et al. 2013).

## Retention of Genetic Diversity

The rate at which genetic diversity is lost from populations is directly related to generation time and the size of the breeding population (Allendorf and Luikart 2007). Increased loss of genetic diversity can occur from non-random mating, large variations in abundance, skewed sex ratios, and non-random culling that disproportionately


*Bull bison fighting during the breeding season in Yellowstone National Park.*

influences a particular population segment (Pérez-Figueroa et al. 2012). Population substructure, such as distinct breeding herds, can reduce rates of gene flow and the formation of new combinations of genes, as well as result in a non-random harvest or culling of animals that increases the loss of genetic diversity (Allendorf and Luikart 2007; Allendorf et al. 2008). However, population subdivision with moderate dispersal rates among subpopulations can minimize the rate of loss of genetic diversity (Allendorf and Luikart 2007). Thus, the future viability of Yellowstone bison depends on maintaining large enough breeding herds to retain sufficient genetic heterozygosity, allelic diversity, and gene flow to enable bison to adapt to a changing environment (Gross et al. 2006; Freese et al. 2007; Bailey 2013).

*The future viability of Yellowstone bison depends on maintaining large enough breeding herds to retain sufficient genetic heterozygosity, allelic diversity, and gene flow to enable bison to adapt to a changing environment.*

To preserve genetic variation over centuries, the bison conservation initiative by the U.S. Department of the Interior and the North American conservation strategy for bison by the International Union for the Conservation of Nature recommended that population (or subpopulation) sizes should be at least 1,000 bison, with approximately equal sex ratios to ensure considerable competition between breeding bulls (Dratch and Gogan 2010; Gates et al. 2010; Gross et al. 2010). These organizations also defined a wild bison population as one with sufficient numbers to prevent the loss of genetic variation, low levels of cattle introgression, and exposure to some forces of natural selection, including competition for breeding opportunities (Dratch and Gogan 2010; Gates et al. 2010). Currently, bison in Yellowstone are the only population of plains bison that meet these objectives, with more than 1,000 bison congregating in both the central and northern regions of Yellowstone during the breeding season and hundreds of mature males competing for breeding opportunities (Pérez-Figueroa et al. 2012; Bailey 2013). However, analyses considering the importance of male reproductive success and fluctuating population size on the possible loss of genetic variation in Yellowstone bison indicate that it may be prudent to manage for at least 3,000 to 3,500 total bison over decades to preserve existing diversity for hundreds of years (Pérez-Figueroa et al. 2012). Though these estimates are derived from the best available information, they incorporate a fair amount of uncertainty due to the lack of validation over many bison generations and across variations in abundance. Thus, this is an area of active research by scientists. There are currently minor concerns about the introgression of cattle genes into Yellowstone bison given that spatial and temporal separation is maintained between them and few cattle wander into the park. However, such concerns may amplify if and when bison are tolerated outside the park during summer and autumn and cattle are grazed in nearby areas.

Intensive management actions near the boundary of Yellowstone National Park to reduce the risk of brucellosis transmission to cattle could potentially result in a substantial loss of genetic diversity in Yellowstone bison and affect population substructure (Halbert 2003; Gates and Broberg 2011; Halbert et al. 2012; Bailey 2013). Sporadic culls of more than 1,000 bison in some winters differentially affected bison from the central region by removing more females and dampening productivity (White et al. 2011; Treanor et al. 2013). Similar non-random culls could differentially influence the genotype diversity and allelic distributions of bison living in the central and northern regions of the park (Halbert et al. 2012). Therefore, managers agreed to minimize future large-scale culls of bison, evaluate how the genetic integrity of bison may be affected by management removals, and assess the genetic diversity necessary to maintain a robust population that is able to adapt to future conditions (USDI, NPS et al. 2008; Pérez-Figueroa et al. 2012; White and Wallen 2012). In addition, the National Park Service developed a rigorous monitoring plan for Yellowstone bison that includes randomly sampling bison from the central and northern regions across decades to identify genetic subdivisions and estimate gene flow within the population (White et al. 2014). Furthermore, each winter biologists use radio telemetry, ground observations, and aerial distribution surveys to track movements of bison and attempt to differentiate animals from the central and northern regions when they approach the boundary of the park and become subject to management actions (White and Wallen 2012).

This approach does not provide absolute certainty with respect to region of origin, but it has been relatively effective for estimating the proportion of culls from bison breeding in each region (White et al. 2011).

Some scientists maintain the National Park Service should actively manage to preserve genetic differences between bison in the central and northern regions of Yellowstone (Halbert et al. 2012). We agree the conservation of genetic diversity is extremely important, but question whether the preservation of a population or genetic substructure created and facilitated by humans should be the goal (White and Wallen 2012). Rather, we propose ecological processes such as natural selection, migration, and dispersal be allowed to prevail and influence how the population and genetic substructure is maintained into the future (White and Wallen 2012). Bison from the central region of Yellowstone began dispersing to northern Yellowstone in the 1980s and dispersal movements between these regions have increased in the past decade (Fuller et al. 2007a; Geremia et al. 2011; White and Wallen 2012). Gene flow between these regions could lessen the effects of population substructure and non-random culling on the loss of genetic diversity (Wallen et al. 2013). Current management actions attempt to preserve bison migration to essential winter range areas within and adjacent to Yellowstone National Park, as well as bison dispersal between the central and northern regions, which bison reestablished after a century of protection, husbandry, and intensive management (White et al. 2011). The current population distribution and genetic substructure may or may not be sustained over time through ecological and evolutionary processes (White and Wallen 2012). The bison will determine that.

## Conclusions

Debate about the population or breeding herd sizes necessary to preserve genetic diversity in Yellowstone bison is contentious at times, and has been included in litigation proceedings (e.g., U.S. District Court for the District of Montana, Missoula Division 2011). Genetic variation is influenced by the interactions of: (1) natural selection for individuals that survive environmental variability, (2) gene flow through movement of individuals between populations, (3) mutations that occur on the DNA of individuals, and (4) genetic drift due to the random nature of mating (Allendorf and Luikart 2007). Some genetic change due to culling by humans is inevitable (Allendorf et al. 2008). Removals of Yellowstone bison via non-random harvest or culling have the potential to cause genetic change by altering population-wide allele frequencies and population subdivision characteristics (Halbert et al. 2012). However, the maintenance of large breeding herds and total population size, along with monitoring genetic diversity over time, will provide managers with information regarding the influence of management actions on genetic diversity (White and Wallen 2012; Wallen et al. 2013). Given the importance of male reproductive success and population size on the loss of genetic variation, we recommend managing for at least 3,000 to 3,500 total bison over decades, while minimizing selective culling and preserving opportunities for bison migration and dispersal between the central and northern regions of the park (Pérez-Figueroa et al. 2012). These genetic objectives should be revised over time as new information is gained.


NPS/Jim Peaco

*Lakota Sioux spiritual leaders conduct a ceremony in the northern region of Yellowstone National Park to honor bison.*

# Chapter 9

## CULTURAL IMPORTANCE

*Rick L. Wallen, P.J. White, and Tobin W. Roop*

Portions of the Great Plains and Rocky Mountains in the Yellowstone area were part of the natural range of bison from prehistoric times. This region is also the homeland of various native peoples who hunted bison as herds moved across the landscape. Archeological evidence indicates the earliest human occupation in the Greater Yellowstone Area occurred about 11,000 years ago, though the oral history of some American Indian tribes suggests they occupied the lands much longer (Nabokov and Loendorf 2002, 2004). At least 10 tribes lived and hunted in the Greater Yellowstone Area during both historic and prehistoric times, including the Crow, Eastern Shoshone, Salish and Kootenai, Shoshone-Bannock, Blackfeet, Nez Perce, Northern Arapaho, and Northern Cheyenne (Nabokov and Loendorf 2002, 2004). An additional 16 American Indian tribes claim association with the Yellowstone region and some First Nations of Canada (Blackfoot, Blood, Piegan, and Assiniboine) also hunted in the region. As late as the 1880s, a band of Shoshone known as the Sheepeaters occupied portions of the area designated as Yellowstone National Park in 1872 (Nabokov and Loendorf 2002, 2004).[7]

After westward expansion by Euro-Americans, treaties with the U.S. government limited the use of lands within the Greater Yellowstone Area by native peoples. Pursuant to the Treaty of Fort Laramie in 1851, the areas now known as Yellowstone National Park, Gallatin National Forest, Bridger-Teton National Forest, and Shoshone National Forest were reserved for some Plains Indian tribes. The land west of the Yellowstone River was used by the Blackfeet tribes (Piegan and Blood), land to the southeast was part of the Crow territory, and land near the upper Missouri River was a common hunting area for those tribes and the Gros Ventre, Flathead, Upper Pend d'Oreille, Kootenai, and Nez Perce tribes (Nabokov and Loendorf 2002, 2004). Another Fort Laramie Treaty in 1868 removed much of this land from tribal control, but allowed hunting by the tribes on open and unclaimed federal lands (Nabokov and Loendorf 2002, 2004). Treaties with the Shoshone-Bannock tribes did not mention the Yellowstone area, but did reference hunting on open and unclaimed lands in the United States. These tribes lived and hunted in the Yellowstone area until the end of the 19th century (Nabokov and Loendorf 2002, 2004). By the 1870s, most tribes were decimated by disease and rapid cultural change, disorganized, and merely trying to survive Euro-American expansion. After Yellowstone National Park was established in 1872, administrators actively discouraged native peoples from using the park, thereby ensuring their influences on the landscape waned and eventually disappeared (Nabokov and Loendorf 2002, 2004).

*Bison are considered ancestors and relatives by some tribes who, in response for the gift of life provided by bison, retain an obligation to serve as their guardians.*

## Importance of Bison to Native Peoples

Bison were central to the culture of native peoples living or hunting in the Yellowstone area because they provided food, clothing, fuel, tools, shelter, and spiritual value. However, the slaughter of bison herds by colonizing Euro-Americans altered this relationship and resulted in

7 Portions of this chapter regarding native peoples and bison were adapted from USDI, NPS (2010, 2014).

decimated, localized populations of both bison and American Indians (Isenberg 2000). Yellowstone bison are special to many tribes because they are the last living link to the indigenous herds of bison that once roamed across North America (USDI, NPS 2010). These tribes view Yellowstone bison as inextricably linked to their existence and survival as indigenous peoples (Plumb and Sucec 2006). The bison are considered ancestors and relatives by some tribes who, in response for the gift of life provided by bison, retain an obligation to serve as their guardians (Plumb and Sucec 2006). Bison represent power and strength and are sometimes viewed as an earthly link to the spiritual world (USDI, NPS 2010).

Some American Indians believe Yellowstone bison have been treated unjustly, similar to native peoples during Euro-American colonization of this country (USDI, NPS 2010). They accurately point out Yellowstone bison are managed differently than other wildlife because some individuals have brucellosis, while elk infected with the same disease are not subject to similar actions (USDI, NPS 2010). As a result, some native people believe the treatment of bison reflects sentiments towards American Indians (Stone 2013). The management of Yellowstone bison has also elicited protests by tribal members and governments (Ruppert 1997). In 1999, approximately 50 American Indians representing several tribes walked from Rapid City, South Dakota to the north entrance of Yellowstone National Park. They performed a ceremony honoring Yellowstone bison that included cutting the flesh on the backs of some tribal members and traditional songs and prayers (Joss 1999; Tarka and Sattler 2008).

The federal government is charged with acting in the best interest (i.e., trust responsibility) of American Indian tribes to protect aboriginal and treaty rights that stem from their original occupation of the land and negotiated and written treaties with the United States government (Meyers 1991; Garrott 2014). The National Park Service consults with 26 American Indian tribes that claim some level of association with Yellowstone National Park (Figure 9.1). Twenty of these 26 groups are current members of the InterTribal Buffalo Council, which is a federally chartered organization established in 1990 to restore bison to American Indian tribes. Another 50 plus tribes across the United States have some interest in bison management. Tribal representatives have related many concerns about the management of Yellowstone bison, including: (1) respectful treatment of the bison, (2), allowing bison to roam freely without fencing or hazing, (3) transferring brucellosis-free bison to the tribes, (4) distributing meat, skulls, and hides of bison that are killed to the tribes, (5) preservation of wickiups, stone alignments, and other cultural features associated with bison, and (6) employment of tribal interns in bison management programs (USDI, NPS 2010).

The frequent occurrence of diabetes on American Indian reservations has motivated a return to a more-traditional, bison-based diet in recent years. As a result, meat from bison culled inside Yellowstone National Park is distributed primarily to American Indian tribes. During 2008, for example, about 258,548 kilograms or 570,000 pounds of bison meat was distributed to 46 tribes and civic food banks (Lewis et al. 2009). The National Park Service currently has agreements with three tribes and a tribal organization to periodically provide them with Yellowstone bison for direct transfer to approved meat processing facilities and subsequent distribution of meat, hides, horns, and other bison parts to their members. Also, several tribes conduct subsistence hunts for bison on open and unclaimed federal lands adjacent to the park in Montana (MFWP 2006a,b, 2009, 2010b). In addition, the National Park Service and several American Indian tribes are exploring the establishment of quarantine facilities where Yellowstone bison can undergo testing for exposure to *Brucella* bacteria and be released elsewhere if they repeatedly test negative (Salazar 2012).

## Euro-American Colonization

Bison also define the Euro-American experience because they were central to national expansion and their products were important elements of trade. Bison occupied the landscape of the Great Plains in large numbers (25 to 30 million by some accounts; Shaw 1995; McHugh 1972; Lott 2002). Early pioneers used bison trails to traverse the landscape, dung to build cooking fires, meat for food, and hides to make clothes and blankets (Isenberg 2000). By 1820, bison became a marketable commodity and great numbers were killed so their hides could be exported to the eastern United States and Europe (Hornaday 1889). Also, the government learned that many tribal cultures depended on bison for their subsistence, and used this information to exploit and conquer them (Wooster 1988; Isenberg 2000).

As numbers of plains bison dwindled, several people captured a few animals to preserve the species (Coder 1975; Isenberg 2000). For example, a Pend d'Oreille Indian named Walking Coyote brought four calves across the continental divide to the Flathead Valley of Montana, where they were propagated by Michel Pablo and the descendants of Charles Allard. Some of these bison were later reintroduced into the northern portion of Yellowstone National Park (Cahalane 1944). In addition, the U.S. Army protected a small indigenous herd of bison that survived in the central region of Yellowstone (Cahalane 1944). Public sentiment to prevent the extinction of bison was widespread and restoration efforts gained momentum after the Lacey Act of 1894 provided legal protection for bison remaining in Yellowstone (Coder 1975; Gates and Broberg 2011). Thereafter, the American Bison Society, Bronx Zoo, and the New York Zoological Society initiated programs to propagate and restore bison elsewhere (American Bison Society 1909; Hornaday 1921; Coder 1975).

The debate over bison conservation contributed significantly to the development of our national conservation ethic based on public ownership of wildlife and the national park system (Plumb and Sucec 2006). Congress clearly indicated that the purpose of national parks is to preserve cultural and natural resources, and bison became a symbol of this ideal. Bison restoration at Yellowstone National Park was underway by 1902, and in 1913 plains bison were introduced to the Wind Cave Game Preserve, which was later incorporated into Wind Cave National Park (Sellars 1997). Thereafter, the American Bison Society continued to establish preserves across the former range of the species. Because bison were a well-known symbol for

NPS/Neal Herbert

conservation, the National Park Service included a bison on its emblem in 1952 (Workman 1997).

## The Changing West

Many wildlife species are highly valued in rural areas of western North America, and sportsman in these communities have been instrumental in their conservation and restoration—including in the Greater Yellowstone Area (e.g., Picton and Lonner 2010). Agriculture, mining, and timber harvest are traditional occupations and important to the economy (Montana Department of Commerce 2006; Bidwell 2010). People are well aware that their livelihoods depend on conserving the natural environment, but a good economy is often a higher priority when conflicts arise (Bergstrom and Harrington 2013). As a result, large ungulates like bison can be considered direct competitors for a valuable commodity—real estate and the grass that grows there (Isenberg 2002; Lott 2002; Franke 2005). Also, ranchers are more likely than other residents to believe that bison will infect cattle with brucellosis (Morris and McBeth 2003). Therefore, restoring wild bison to public lands is an appalling thought to some people because it is seen as a detriment to the economy and a threat to their way of life, property rights, and ability to graze cattle on public lands (McDonald 2001; Bienen and Tabor 2006). Likewise, some members of American Indian tribes prefer to raise livestock to feed their families and generate income, rather than restore wild bison to tribal lands (Hatfield et al. 2013).

In recent decades, many rural areas in the intermountain west have become more demographically and economically diverse, with recreation, tourism, and amenity living competing with agriculture and natural resource extraction economies (Haggerty and Travis 2006; Hansen 2009). The Greater Yellowstone Area is no exception and many new residents are migrants from other regions across the country where living with wildlife is a novelty (Hansen et al. 2002; Johnson and Stewart 2005). As a result, more residents in these communities now consider the environment and wildlife viewing to be primary economic assets (Morris and McBeth 2003). These residents are also less likely to believe that bison will transmit brucellosis to cattle (Morris and McBeth 2003). Hence, there are often differences of opinion about bison management between residents that are tourism-based and those that are agricultural-based (Bergstrom and Harrington 2013).

While these portrayals are exaggerated (Robbins 2006; Bidwell 2010), there is little doubt tourism is now a major driver of the economy in the Greater Yellowstone Area. Visitors to national parks and other public lands provide substantial economic influx to surrounding communities (Cullinane Thomas et al. 2014). For example, visitors to Yellowstone National Park during 2012 spent more than $400 million in local communities, which supported about 5,600 jobs and generated $473 million in combined visitor and workforce sales (value of industry production/output), $165 million in labor income (wages, salaries, payroll benefits), and $272 million in value added (labor income plus profits, rents, and sales and excise taxes; Cullinane Thomas et al. 2014). About 50 percent of surveyed resident and non-resident visitors indicated seeing bison was a reason for their trip, and about 5 percent said they would not have come to the area if bison had not been present (Duffield et al. 2000a,b).

## Conclusions

Despite their biological and cultural importance, bison are the only wild North American ungulate that has not been recovered across significant portions of their historic range (Lott 2002; Freese et al. 2007; Bailey 2013). Unlike bighorn sheep, caribou, deer, elk, moose, mountain goats (*Oreamnos americanus*), and pronghorn (*Antilocapra americana*), bison receive little tolerance on private or public lands outside of national parks and refuges. Thus, they have failed to gain legitimate status as wide-ranging wildlife and their conservation is constrained by real and perceived conflicts (Lott 2002; Plumb and Sucec 2006; Bailey 2013). For most of the 20th century, as Yellowstone bison recovered from near extirpation, they did not regularly and extensively venture outside Yellowstone National Park (Meagher 1973). This led to the beliefs bison should remain in the park, and they only leave when large numbers overgraze the grasslands (Plumb et al. 2009; Becker et al. 2013). These beliefs have been reflected in the treatment of bison as livestock in many areas outside the park (Franke 2005; Plumb et al. 2009; Bailey 2013; Becker et al. 2013).

Conflicts between agricultural, political, and wildlife conservation values are a century old challenge for society. The most successful wildlife conservation measures account for the diversity of values held by society, and conflicts are resolved through education, negotiation, and creative actions. As the United States progresses further into the third century of its existence, acknowledgment of the historical conditions that challenged native peoples and Euro-American pioneers will be an important cultural value to society. Also, preservation of one of the last unfenced, wide-ranging bison populations subject to nearly all the evolutionary pressures from which their descendants evolved would be a tremendous achievement that could invigorate the restoration of the ecological role of plains bison as a species in western North America (USDI, NPS 2011; Bailey 2013). As a worldwide leader in wildlife conservation, the National Park Service will continue to advocate for the conservation of wild bison and the processes that sustain them at ecosystem scales. Long-term success in this endeavor will come through effective partnerships with American Indian tribes, federal and state agencies, private landowners, and other interested stakeholders that incrementally increase tolerance for bison in more areas based on successful management that addresses concerns and allows people's perceptions of these icons of western America to change (White et al. 2013c).

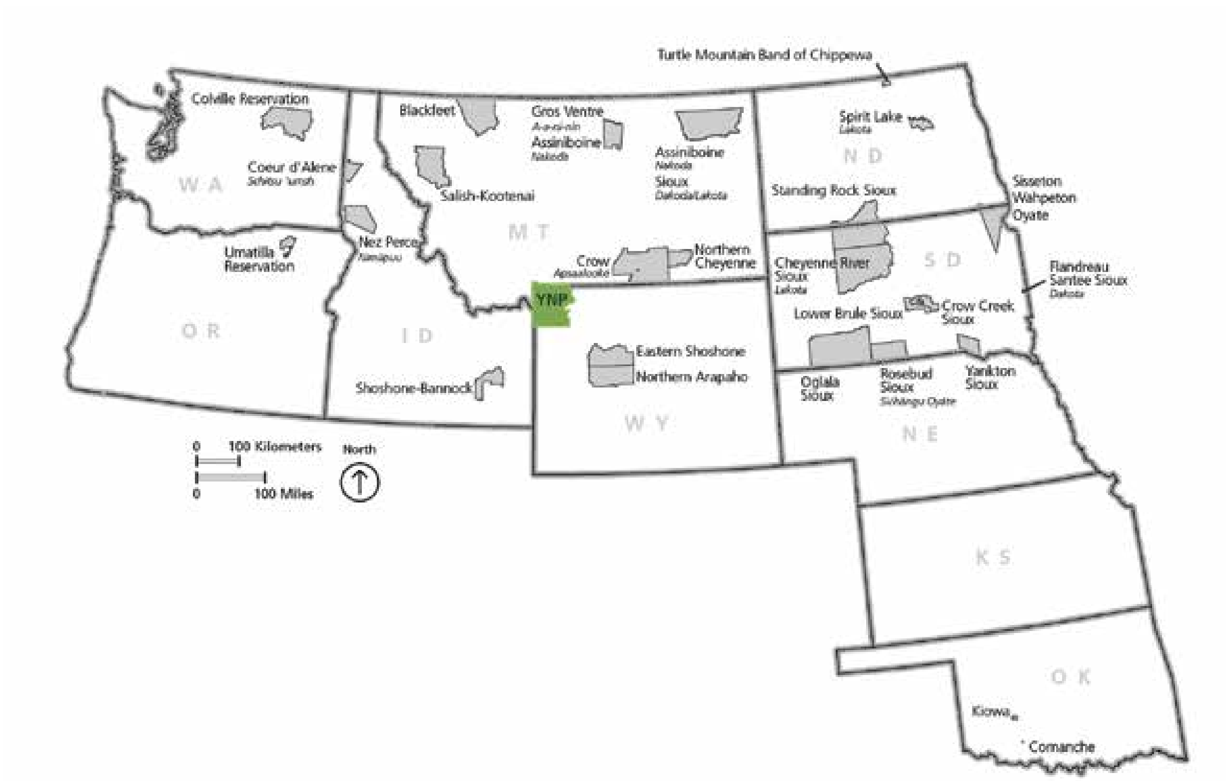


*Figure 9.1. American Indian tribes associated with Yellowstone National Park (YNP).*


*Staff on horseback hazing bison near Undine Falls in the northern region of Yellowstone National Park.*

# Chapter 10

## CURRENT MANAGEMENT—ATTEMPTING TO BALANCE CONSERVATION WITH DISEASE CONCERNS

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The restoration of Yellowstone bison has been extremely successful, with many scientists considering them the only ecologically viable population of plains bison in the United States (Freese et al. 2007; Sanderson et al. 2008; Gates et al. 2010). There is local and national support for allowing these wild bison to migrate and disperse to new areas outside Yellowstone National Park (Franke 2005; Bailey 2013). However, there is also substantial resistance to this prospect, especially from the local agricultural community (Montana Sixth Judicial Court, Park County 2013). Managing these massive, unfenced, wild animals in close proximity to humans can be challenging at times and involve substantial investments of time, effort, and money to keep bison away from areas where they are not tolerated. Moreover, there are concerns about the safety of humans near bison; damage to property such as fencing, landscaping, and vehicles; overgrazing of habitats also used by livestock and other wild ungulates; and brucellosis transmission to cattle (Lott 2002; Boyd 2003; Rhyan et al. 2009).

## Interagency Bison Management Plan

Due to these concerns, the federal government and the State of Montana agreed in 1992 to prepare a long-term management plan for Yellowstone bison. Progress on the plan was slower than anticipated, and in 1995, the State sued the National Park Service and the Animal and Plant Health Inspection Service over the delay. The parties subsequently agreed to a schedule for completing the plan, and a draft was developed and released for public review in 1998. After reviewing public comments, the federal agencies presented a modified plan to the State that allowed for a larger bison population and greater tolerance for bison outside the park. The State did not agree and the parties engaged a mediator to help resolve their differences. This mediation resulted in the completion of the Interagency Bison Management Plan in 2000 that established guidelines for cooperatively managing the risk of brucellosis transmission from Yellowstone bison to cattle, while conserving a wild bison population and allowing some bison to occupy winter ranges on public lands in Montana (USDI, NPS and USDA, USFS, APHIS 2000a; see Chapter 3 for details).

When the Interagency Bison Management Plan was developed, the State of Montana was under tremendous pressure to keep brucellosis out of livestock to comply with free trade agreements benefitting the cattle industry (Bidwell 2010). Therefore, any chance of brucellosis transmission from bison to cattle was unacceptable to livestock regulators (Bidwell 2010). In fact, regulators and elected officials intensified misperceptions that Yellowstone bison posed a high risk to cattle by transferring authority for bison management in Montana from wildlife to livestock managers and making the brucellosis-free status of livestock a condition in trade agreements (Bidwell 2010). These misperceptions and actions had substantial impacts on the management of Yellowstone bison because the Interagency Bison Management Plan is primarily about minimizing the risk of brucellosis transmission to cattle, not the conservation and restoration of bison (Keiter 1997; Bidwell 2010).

Since 2000, many circumstances that influenced the derivation and implementation of the Interagency Bison Management Plan have changed, and scientific knowledge regarding bison and brucellosis has improved substantially. These changes and advances are summarized in the following bullets (see Chapters 2 and 3 for details and citations):

- Four American Indian Tribes asserted their treaty rights to conduct subsistence hunts of bison in southwestern Montana.
- There are fewer cattle adjacent to Yellowstone National Park, particularly on the Royal Teton Ranch (north) and Horse Butte (west). Also, cattle grazing may be delayed on the Watkins Creek and South Fork allotments (west) if bison are present.
- The Animal and Plant Health Inspection Service implemented regulations whereby brucellosis outbreaks in cattle are dealt with on a herd-by-herd basis. As a result, the entire state does not lose its class-free brucellosis status due to one or more outbreaks.
- The states of Idaho, Montana, and Wyoming designated surveillance areas for brucellosis that were defined by occurrence of the disease in elk. These areas benefit the livestock industry because producers therein are reimbursed for brucellosis testing costs and unnecessary testing is not required elsewhere in the states.
- Calf-hood vaccination of cattle has been implemented with high compliance in the designated surveillance area in Montana.
- Experimental studies indicated bull bison are not brucellosis transmission vectors.
- The prevalence of brucellosis in elk and the frequency of transmission from elk to cattle have increased. As a result, several independent studies determined that the risk of brucellosis transmission from bison to cattle was minute compared to the risk from elk.

- A quarantine feasibility study was conducted and successful, with the surviving bison and their offspring being declared brucellosis free and transferred elsewhere for conservation and cultural purposes.
- There were significant changes in bison movement patterns and distribution, with more bison migrating and dispersing to the northern portion of the park. Large migrations into Montana during severe winters resulted in property damage and human safety concerns, as well as large culls of bison.
- There was increased concern by bison managers, American Indian tribes, and the public about killing bison in the third trimester of pregnancy.
- Studies indicated many older bison testing positive for brucellosis exposure were no longer infectious and may have some resistance to the disease if reexposed.
- American Indian tribes and a tribal organization became involved with the management of Yellowstone bison, including developing an annual operating plan, conducting subsistence hunts, relocating brucellosis-free bison to tribal lands, and distributing meat, hides, and horns from culled animals to their members.
- Several independent evaluations recognized that the substantial suppression of brucellosis through vaccination would be extremely difficult with existing vaccines and delivery technologies. As a result, the National Park Service decided not to initiate the remote vaccination of bison.

These changed circumstances and improved knowledge led to several adaptive management adjustments to the Interagency Bison Management Plan. Annual public and tribal hunts were initiated in Montana. Actions such as strategic hazing of bison from conflict areas to suitable habitat, and financial aid for fencing, were implemented to reduce conflict with landowners and livestock operators. In addition, there was increased tolerance for more bison in Montana across a larger conservation area, especially for bull bison due to their lower risk of brucellosis transmission. Furthermore, managers attempted to reduce shipments of bison to meat processing plants by using alternate tools such as hazing, hunting, and increased tolerance. Details of these adaptive adjustments are provided in Chapter 3.

## Management Tools and Operations

The adjusted Interagency Bison Management Plan has three categories of objectives: (1) conserve a viable population of wild bison, (2) prevent brucellosis transmission from bison to cattle, and (3) reduce the prevalence of brucellosis in bison. Bison numbers are supposed to be regulated near an end-of-winter guideline of 3,000 (USDI, NPS and USDA, USFS, APHIS 2000a; Interagency Bison Management Plan Partner Agencies 2006). During June and July, biologists conduct counts and age and gender classifications of bison in the central and northern regions of Yellowstone (Hess 2002; Tables 10.1 and 10.2). Biologists then use long-term weather forecasts and population and migration models to predict bison abundance and composition by region at the end of the upcoming winter, as well as the numbers of bison likely to migrate to the park boundary (Geremia et al. 2013, 2014a). The partners use these predictions to establish annual removal objectives for bison based on abundance, distribution, and demographic goals. During the following winter, biologists use aerial and ground counts, snow model projections, and revised weather forecasts to refine predictions of the timing and magnitude of bison migrations and support decision-making (Interagency Bison Management Plan Members 2013).[8]

A variety of management tools are used to reduce bison numbers towards 3,000, including: (1) public and treaty harvests in Montana, (2) capture and culling near the park boundary, and (3) shooting or capture in Montana. Captured bison are shipped to meat processing or research facilities. No quarantine facilities or terminal pastures are currently operational. Biologists monitor bison abundance through the winter and compile information on hunter harvest, management culls, predation off-take, and winter-kill. If numbers of bison decrease to

8 Portions of this section contain excerpts, with permission, from various documents written in collaboration with the other members involved with the Interagency Bison Management Plan. The cited documents are available at http://ibmp.info/.

| | | Central herd | | | Northern herd | | |
|---|---|---|---|---|---|---|---|
| | | Total | Adults | Calves | Total | Adults | Calves |
| 2000 | June 4, 2000 | 2,060 | 1,734 | 326 | 553 | 460 | 93 |
| | July 13, 2000 | 2,118 | | | 590 | | |
| | August 31, 2000 | 2,084 | | | 529 | | |
| 2001 | June 21, 2001 | 2,599 | 2,190 | 469 | 657 | 553 | 104 |
| | July 25, 2001 | 2,564 | | | 719 | | |
| 2002 | June 25, 2002 | 3,100 | 2,560 | 540 | 548 | 477 | 71 |
| | July 29, 2002 | 2,901 | | | 813 | | |
| | August 22, 2002 | 3,238 | | | 807 | | |
| 2003 | July 10, 2003 | 2,905 | 2,471 | 434 | 873 | 748 | 125 |
| | August 8, 2003 | 2,923 | | | 888 | | |
| | August 28, 2003 | 2,772 | | | 994 | | |
| 2004 | July 21, 2004 | 2,811 | 2,310 | 501 | 1,337 | | |
| | July 28, 2004 | 3,027 | | | 968 | | |
| | August 4, 2004 | 3,339 | | | 876 | | |
| 2005 | July 19, 2005 | 3,553 | | | 1,266 | | |
| | July 26, 2005 | 3,394 | | | 1,353 | | |
| | August 1, 2005 | 3,531 | | | 1,484 | | |
| 2006 | July 19, 2006 | 2,430 | 2,146 | 284 | 1,283 | | |
| | July 26, 2006 | 2,512 | | | 1,377 | | |
| | August 2, 2006 | 2,496 | | | 1,279 | | |
| 2007 | June 14, 2007 | 2,734 | 2,385 | 349 | 1,820 | 1,499 | 321 |
| | July 30, 2007 | 2,390 | | | 1,569 | | |
| | August 6, 2007 | 2,624 | | | 2,070 | | |
| 2008 | June 14, 2008 | 1,115 | 1,052 | 103 | 1,788 | 1,463 | 325 |
| | July 8, 2008 | 1,540 | | | 1,341 | | |
| | July 15, 2008 | 1,469 | | | 1,500 | | |
| 2009 | June 12, 2009 | 1,462 | 1,293 | 169 | 1,839 | 1,520 | 319 |
| | July 9, 2009 | 1,544 | | | 1,433 | | |
| | July 16, 2009 | 1,535 | | | 1,648 | | |
| 2010 | June 14, 2010 | 1,653 | 1,426 | 227 | 2,245 | 1,890 | 355 |
| | July 8, 2010 | 1,735 | | | 1,980 | | |
| | July 22, 2010 | 1,713 | | | 1,850 | | |

| | | Central herd | | | Northern herd | | |
|---|---|---|---|---|---|---|---|
| | | Total | Adults | Calves | Total | Adults | Calves |
| 2011 | June 21, 2011 | 976 | 880 | 96 | 2,675 | 2,188 | 487 |
| | July 18, 2011 | 1,406 | | | 2,314 | | |
| | July 25, 2011 | 1,335 | | | 2,150 | | |
| 2012 | June 21, 2012 | 1,389 | 1,188 | 201 | 2,496 | 2,103 | 393 |
| | July 8, 2012 | 1,640 | | | 2,531 | | |
| | July 22, 2012 | 1,561 | | | 2,669 | | |
| 2013 | June 6, 2013 | 1,338 | 1170 | 168 | 3,154 | 2,620 | 534 |
| | July 15, 2013 | 1,504 | | | 3,420 | | |
| | July 22, 2013 | 1,337 | | | 3,228 | | |
| 2014 | June 20, 2014 | 1,338 | 1,190 | 148 | 3,519 | 2,928 | 591 |
| | July 18, 2014 | 1,448 | | | 2,938 | | |
| | July 25, 2014 | 1,444 | | | 3,421 | | |

*Table 10.1. Annual counts of bison in the central and northern regions of Yellowstone National Park during June through August from 2000 to 2014 (Geremia et al. 2014a).*

2,300, managers have agreed to increase the use of non-lethal management measures. If numbers decrease to 2,100, managers would cease harvests and management removals and use non-lethal measures to maintain separation between bison and cattle (USDI, NPS et al. 2008).

Bison numbers and their distribution in Montana are managed under the authority and discretion of the state veterinarian due to their chronic exposure to brucellosis (81-2-120 Montana Code Annotated 2011). The distribution of wild bison in Montana is currently limited to certain lands located north (Gardiner basin) and west (Hebgen basin) of the park. Bison can move onto National Forest System and other lands north of the park boundary and south of Yankee Jim Canyon (Figure 10.1) each winter and spring. Bison are not allowed north of the mountain ridge-tops between Dome Mountain/Paradise Valley and the Gardiner basin on the east side of the Yellowstone River and

Tom Miner basin and the Gardiner basin on the west side of the Yellowstone River (MFWP and MDOL 2012). Bison approaching these areas are hazed to other available habitat within the tolerance area, captured, or killed. In addition, bison can move into the Absaroka-Beartooth Wilderness north of the park, including the upper portions of Hellroaring and Slough Creek. West of Yellowstone National Park, bison are allowed to move onto the Horse Butte peninsula at the east end of Hebgen Lake and other nearby areas (USDI, NPS et al. 2008; Figure 10.2). Bison can also use the Eagle Creek/Bear Creek area, Cabin Creek Recreation and Wildlife Management Area, and the Monument Mountain Unit of the Lee Metcalf Wilderness year-round (USDI, NPS and USDA, USFS, APHIS 2000a,b).

*The restoration of Yellowstone bison has been extremely successful, with many scientists considering them the only ecologically and genetically viable population of plains bison in the United States.*

Hunting outside Yellowstone National Park is used to manage the abundance and distribution of bison in Montana, while providing sport and subsistence harvest opportunities and cultural and spiritual engagement (Interagency Bison Management Plan Members 2013). Each year, Montana Fish, Wildlife & Parks allocates permits for bison hunting from November 15 through February 15 in the northern and western management areas (MFWP and MDOL 2004). Also, American Indian tribes (Confederated Salish and Kootenai Tribes of the Flathead Nation, Nez Perce Tribe, Confederated Tribes of the Umatilla Reservation, and Shoshone-Bannock Tribes) have rights, reserved through treaties with the U.S. Government, to hunt bison on certain federal lands in southwestern Montana (MFWP 2006a,b, 2009, 2010b). Montana Fish, Wildlife & Parks and these tribes coordinate each summer regarding bison removal objectives, permits, and harvests. Also, they enforce regulations and permit requirements for their respective hunters by sending game wardens to oversee hunts (Interagency Bison Management Plan Members 2013).

State and federal employees haze bison to prevent mingling with cattle, ensure human safety, prevent property damage, and prevent the movement of bison outside of agreed-upon tolerance zones or onto private property where landowners do not want bison. Hazing is accomplished primarily on horseback, but all-terrain vehicles, snowmobiles, and helicopters may be used at times (Interagency Bison Management Plan Members 2013). Managers attempt to minimize hazing in areas where hunting is ongoing. The partners involved with the plan coordinate in April to compile information on bison movements and distribution, snow conditions, vegetation green-up, river flows, logistical issues (e.g., staff, horse, and helicopter availability; traffic control; visitation and road closures), and dates and locations where cattle will be released for summer grazing (Interagency Bison Management Plan Members 2013). Based on this information, the partners devise a plan for hazing bison from the northern management area (Gardiner basin) back into Yellowstone National Park near a target date of May 1. They also devise a plan for hazing bison from the western management area (Hebgen basin) back into the park near a target date of May 15. These operations could occur earlier than the target dates if forage and other conditions at higher elevations in Yellowstone National Park are suitable or later if conditions preclude safe and effective movements of bison to habitats that will hold/sustain them. To avoid multiple hazing operations, the partners are exploring private land management options with willing landowners, including conservation easements, livestock grazing plans, and strategic fencing to separate livestock and bison.

Bison have been captured (1) for brucellosis testing and vaccination, (2) to cull bison infected with brucellosis, (3) to reduce bison numbers, (4) because they have repeatedly resisted hazing to keep them within agreed-upon tolerance zones, and (5) because there were already large numbers of bison in the tolerance zones and additional bison could induce movements into no-tolerance areas or cause human safety and property damage issues (Interagency Bison Management Plan Members 2013). As necessary, managers attempt to conduct captures before pregnant bison are late in their third trimester (Interagency Bison Management Plan Members 2013). Bison may be moved into capture facilities by hazing and/or through enticement with weed-free hay. The National Park Service maintains a capture and handling facility at Stephens Creek within Yellowstone National Park in the

| Date | | Classified in mixed gender groups by age | | | | | Air count | |
|---|---|---|---|---|---|---|---|---|
| | | Male>1 | Male1 | Female>1 | Female1 | Calf | Bachelor | Mixed |
| July 7-15, 2003 | central | 438 | 150 | 1426 | 241 | 498 | 380 | 2521 |
| | northern | 159 | 23 | 176 | 12 | 46 | 77 | 795 |
| | | 133 | 11 | 227 | 15 | 110 | | |
| July 14-18, 2004 | central | 638 | 179 | 1082 | 126 | 497 | 284 | 2594 |
| | | 523 | 125 | 932 | 131 | 397 | | |
| | northern | 247 | 35 | 331 | 33 | 164 | 125 | 1145 |
| | | 232 | 26 | 458 | 49 | 145 | | |
| July 6-15, 2005 | central | 500 | 178 | 1098 | 162 | 430 | | |
| | | 674 | 175 | 1060 | 148 | 443 | | |
| | northern | 276 | 63 | 441 | 51 | 153 | | |
| | | 205 | 49 | 324 | 37 | 97 | | |
| July 11-13, 2006 | central | 368 | 141 | 654 | 101 | 258 | 518 | 2078 |
| | | 386 | 152 | 757 | 111 | 301 | | |
| | northern | 102 | 27 | 202 | 40 | 103 | | |
| July 10-17, 2007 | central | 375 | 100 | 709 | 109 | 342 | | |
| | | 555 | 119 | 805 | 106 | 305 | | |
| | northern | 300 | 139 | 637 | 101 | 339 | | |
| | | 173 | 28 | 366 | 28 | 169 | | |
| July 8-11, 2008 | central | 116 | 36 | 387 | 50 | 110 | 444 | 1101 |
| | northern | 198 | 87 | 433 | 61 | 232 | 178 | 1158 |
| July 6-16, 2009 | central | 145 | 63 | 427 | 73 | 158 | 480 | 1063 |
| | | 161 | 62 | 498 | 47 | 186 | | |
| | northern | 244 | 84 | 414 | 53 | 237 | 191 | 1239 |
| | | 224 | 83 | 391 | 53 | 179 | | |
| July 6-20, 2010 | central | 340 | 72 | 517 | 57 | 219 | 342 | 1370 |
| | | 369 | 82 | 537 | 81 | 228 | | |
| | northern | 228 | 126 | 934 | 140 | 391 | 20 | 1755 |
| | | 298 | 150 | 679 | 121 | 344 | | |

| Date | | Classified in mixed gender groups by age | | | | | Air count | |
|---|---|---|---|---|---|---|---|---|
| | | Male>1 | Male1 | Female>1 | Female1 | Calf | Bachelor | Mixed |
| July 7-19, 2011 | central | 118 | 58 | 323 | 37 | 105 | 413 | 1407 |
| | | 163 | 53 | 309 | 40 | 106 | | |
| | northern | 303 | 131 | 915 | 99 | 361 | 185 | 2103 |
| July 9-29, 2012 | central | 282 | 68 | 493 | 41 | 173 | 398 | 1242 |
| | | 420 | 80 | 477 | 55 | 216 | 212 | 1349 |
| | northern | 375 | 187 | 876 | 165 | 466 | 80 | 2451 |
| | | 405 | 114 | 698 | 84 | 288 | 50 | 2619 |
| July 15-25, 2013 | central | 287 | 101 | 415 | 82 | 197 | 342 | 1162 |
| | | 372 | 102 | 401 | 77 | 191 | 189 | 1148 |
| | northern | 457 | 231 | 1061 | 191 | 528 | 145 | 3275 |
| | | 608 | 249 | 1149 | 198 | 538 | 77 | 3151 |
| July 14-25, 2014 | central | 275 | 113 | 565 | 69 | 206 | 280 | 1168 |
| | | 296 | 71 | 380 | 63 | 145 | 285 | 1159 |
| | northern | 310 | 155 | 1,023 | 126 | 422 | 141 | 2797 |
| | | 565 | 266 | 1,314 | 259 | 612 | 261 | 3163 |

*Table 10.2. Annual ground and aerial composition surveys of bison in the central and northern regions of Yellowstone National Park during July from 2003 through 2014. Ground composition columns represent total numbers of animals observed in mixed age and sex groups (Geremia et al. 2014a).*

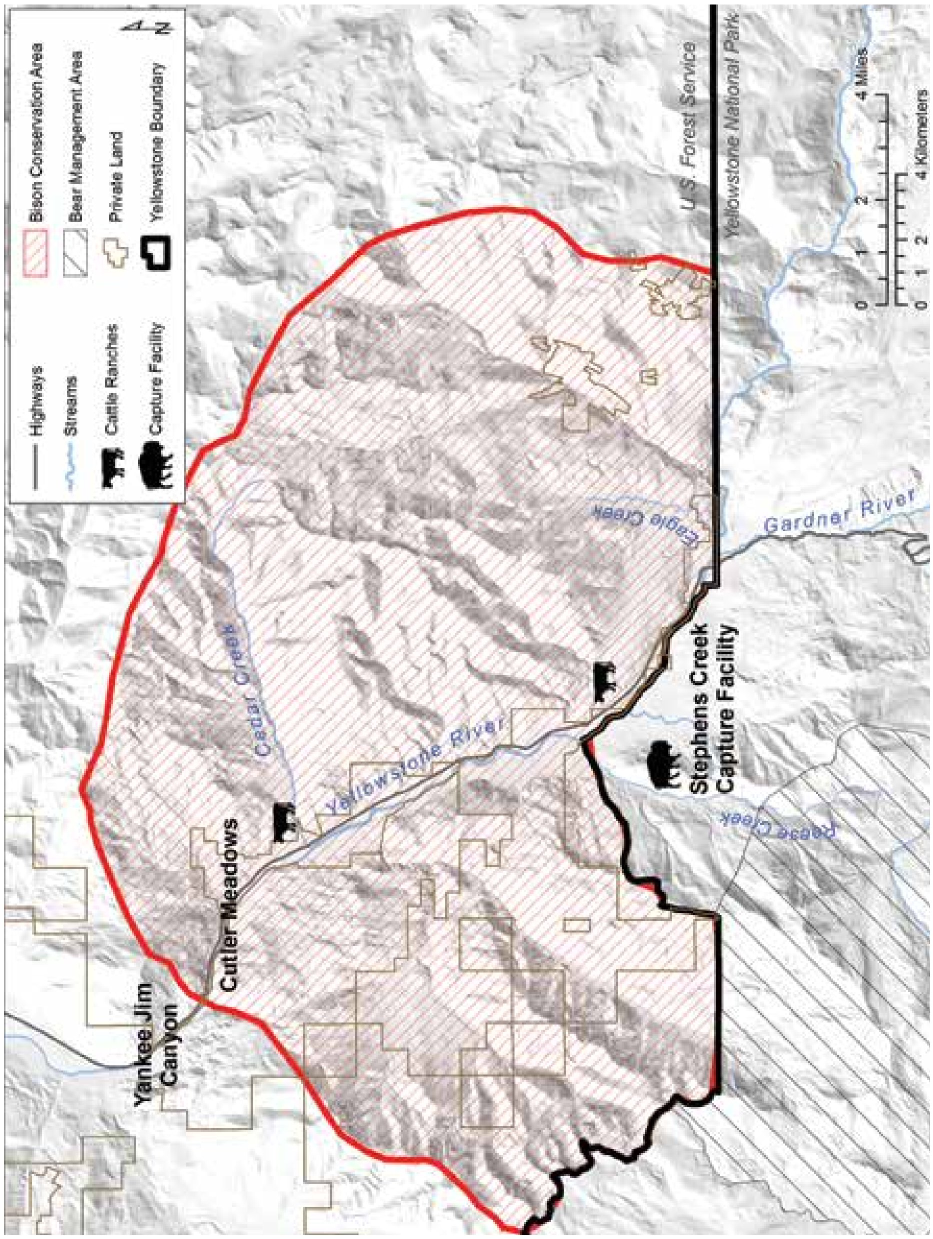


*Figure 10.1. Northern management area for the Interagency Bison Management Plan (IBMP) as adjusted during 2012.*

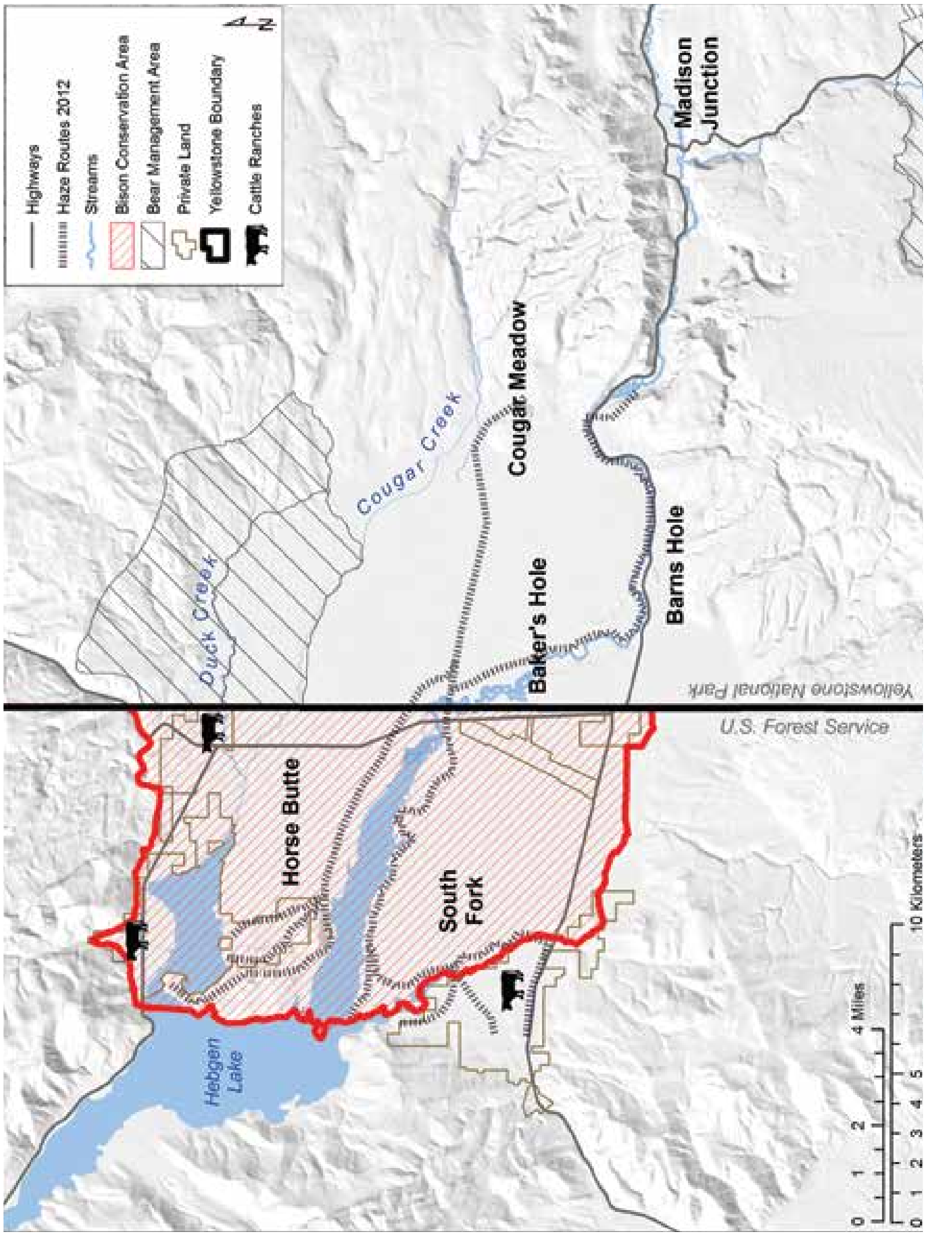


*Figure 10.2. Western management area for the Interagency Bison Management Plan (IBMP).*

northern management area, while the State of Montana could maintain or erect one or more capture and handling facilities outside the park.

The 2000 Interagency Bison Management Plan called for the capture and serological testing of Yellowstone bison for brucellosis exposure, with those testing positive for antibodies to *Brucella abortus* being sent to meat processing facilities and test-negative bison being vaccinated (USDI, NPS and USDA, USFS, APHIS 2000a,b). However, the operations plans for 2013 and 2014 (Interagency Bison Management Plan Members 2013) modified the brucellosis testing and response protocol somewhat to remove likely infectious bison, while retaining and vaccinating other bison to increase resistance to *Brucella* bacteria in the population (Treanor et al. 2010, 2011; Ebinger et al. 2011). When bison are captured and tested for antibodies to *Brucella* in their blood, animals identified as likely infectious could be shipped to meat processing facilities up to the removal objectives for that year to help reduce brucellosis transmission (Interagency Bison Management Plan Members 2013). Bison that have a lower risk of being actively infected, based on negative test results or relatively low age-specific antibody levels for *Brucella*, could be retained in the population (Geremia et al. 2013).

Bison selected for removal from the population are segregated from other bison and transported to meat processing or research facilities as soon as practical after capture and processing. Bison not selected for removal are released from capture facilities when winter weather moderates in spring or earlier to provide operational space and shorten confinement (Interagency Bison Management Plan Members 2013). Prior to their release, calf, yearling, and non-pregnant adult female bison may be vaccinated for brucellosis via syringe with strain RB51. Animals vaccinated with *Brucella* vaccine should not be consumed within 21 days of vaccination; therefore, these animals are generally held within the capture facility for at least this length of time if hunting is ongoing (Interagency Bison Management Plan Members 2013). If it is necessary to retain pregnant, likely infectious bison in captivity, then staff segregate them from susceptible bison until after they have calved and transmission risk is past.

By June 15 each year, the Montana Department of Livestock and the Animal and Plant Health Inspection Service determine the vaccination status of all at-risk cattle in or coming into the Hebgen and Gardiner basins (Interagency Bison Management Plan Members 2013). These agencies use existing regulations and incentives to make sure that all cattle are vaccinated as calves or adults. Furthermore, the partners involved with the Interagency Bison Management Plan meet about three times annually to publicly review, evaluate, and modify operating procedures (see meeting minutes at http://ibmp.info/).

## Accomplishments and Failures

The conservation of Yellowstone bison has been successful under the Interagency Bison Management Plan, with overall abundance ranging between 2,400 and 5,000 (average ≃ 3,900; White et al. 2011; Geremia et al. 2014a). These bison are managed as wildlife and have relatively high genetic variation (Plumb et al. 2009; Halbert et al. 2012). The population is prolific and has recovered rapidly from decreases in abundance due to culling or natural mortality (Fuller et al. 2007b; Geremia et al. 2009; White et al. 2011). Also, adaptive management adjustments during 2005 to 2012 increased tolerance for bison on habitat in Montana by expanding the northern and western management areas and allowing more bison to occupy these areas during winter and spring (MFWP and MDOL 2012). In addition, the transmission of brucellosis from bison to cattle has not occurred, due in part, to successful efforts by federal and state agencies to maintain separation.

However, there has not been a reduction in brucellosis prevalence within the Yellowstone bison population under the Interagency Bison Management Plan. The proportion of adult females that test positive for brucellosis exposure has remained approximately constant at about 60 percent (White et al. 2011; Hobbs et al. 2014). Several of the key assumptions in the plan were faulty or problematic to implement. Expected advances in vaccines, diagnostics, and delivery technologies did not occur, and as a result, the plan overestimated the feasibility and effectiveness of vaccination (White et al. 2011, 2013b). Also, some aspects of the plan such as test-and-slaughter at capture facilities were never completely or consistently implemented for various reasons (see Chapter 2; White et al. 2011). In addition, the plan underestimated bison reproduction and survival rates. As a result, more bison must be removed to regulate the population towards 3,000. This has contributed to a continued reliance on the capture and shipment of bison to meat processing facilities to reduce abundance (White et al. 2011).

In addition, there is no guarantee of continued tolerance for bison in Montana due to disease, political, and social concerns (Boyd 2003; Franke 2005; Bailey 2013). In 2011, the Park County Stockgrowers Association filed a lawsuit to prevent additional tolerance for bison north of the park boundary. Also, during winters 2011 and 2013, the Montana legislature proposed several bills intended to limit the distribution and relocation of wild bison in Montana. Though the court dismissed this lawsuit in 2013 (Montana Sixth Judicial Court, Park County 2013), and to date, these bills have not become law, collectively these actions foretell that there may be little tolerance for bison in areas of Montana not adjacent to Yellowstone National Park, regardless of their vaccination or disease status.

## Conclusions

The successes and failures of the Interagency Bison Management Plan highlight the difficulties associated with managing for two competing objectives—preventing brucellosis transmission from bison to cattle, while conserving a wild population of bison (Treanor et al. 2013). Bison managers implement actions to prevent brucellosis transmission each winter, but unintended effects from these actions on the demography and genetic diversity of bison may not be evident for many years (Treanor et al. 2013). To avoid undercutting conservation efforts, it is important to implement proven and relatively non-intrusive management practices such as maintaining separation between wildlife and cattle at the appropriate time of year to reduce brucellosis transmission risk (Nishi 2010).

Given current conditions and technology, it would be ineffective to implement a vaccination program to suppress brucellosis in wildlife across the entire Greater Yellowstone Area (see Chapter 2). Federal and state agencies have spent approximately $2 million annually to implement the Interagency Bison Management Plan, and another $15 million to purchase land, conservation easements, and grazing rights (U.S. Government Accountability Office 2008; NPS and MFWP 2008). Therefore, it is imperative to develop realistic objectives and rigorous monitoring and research protocols to attain necessary information, measure progress towards objectives, and periodically assess the effects and effectiveness of management actions (U.S. Government Accountability Office 2008; Nishi 2010; White et al. 2013c).


NPS/Neal Herbert

*Watching wild bison*
*in the Lamar Valley of*
*Yellowstone National Park.*

# Chapter 11

## THE FUTURE—RECOMMENDATIONS FOR BISON CONSERVATION

*P.J. White, Rick L. Wallen, Chris Geremia, John J. Treanor, and David E. Hallac*

Yellowstone bison comprise the largest conservation population of plains bison and are one of only a few populations to have continuously occupied portions of their current distribution (Franke 2005; Plumb et al. 2009; Bailey 2013). They are managed as wildlife in multiple large herds that move across extensive portions of the landscape within and near Yellowstone National Park (Plumb et al. 2009; Gates and Broberg 2011; White et al. 2013b). Bison exist on this landscape with a full suite of native ungulates and predators, while being exposed to natural selection factors such as competition for food and mates, predation, and survival in challenging environmental conditions (Becker et al. 2009a,b; Plumb et al. 2009; Geremia et al. 2011; Garrott et al. 2013). As a result, Yellowstone bison have likely retained adaptive capabilities that may be diminished in other bison herds across North America that are managed like domesticated livestock in fenced pastures with human-induced seasonal movements among pastures, no predators, selective culling of older bulls to facilitate easier management, and selection for the retention of rare alleles—the function and importance of which have not been identified (Berger and Cunningham 1994; McDonald 2001; Lott 2002; Franke 2005; Gates et al. 2010; White and Wallen 2012; Bailey 2013). Yellowstone bison also provide meat for predators, scavengers, and decomposers, and allow visitors to observe this symbol of the American frontier in a wild, unfenced setting (Knapp et al. 1999; Franke 2005; Bailey 2013; Frank et al. 2013; Garrott et al. 2013).

## Lingering Issues

Despite this success, the management of bison near the boundary of Yellowstone National Park is unsettling to many people. Park managers are often asked why bison are managed differently from other wildlife and not allowed to move freely into Montana and disperse to new areas. Conversely, other people believe bison should be kept in the park and either managed like livestock or hunted to reduce numbers. Many constituents are adamant that Yellowstone bison are so valuable they should be relocated elsewhere instead of being shipped to meat processing facilities due to concerns about overabundance or brucellosis transmission to cattle.

The debate about how to conserve and manage Yellowstone bison involves a variety of issues, including:

- Abundance—How many is too many (or too few)?
- Brucellosis—What should be done and what can be done to suppress the disease and/or lessen transmission risk to cattle?
- Distribution—Where and when will bison be tolerated outside the park?
- Elk—Should management of brucellosis in elk be considered as well?
- Genetic Integrity—What should be done to preserve existing genetic diversity and population substructure?

- Habitat—Should humans intervene to control ungulate numbers and grazing effects?
- Property Damage and Human Safety—How intensive should management be to minimize risk?
- Wildness —What intensity and types of management are appropriate for migratory wild bison whose core range occurs within a national park?
- Cultural/Economic —What is the optimal abundance and distribution of bison for people that value them, and how much are they willing to invest to realize that value?
- Hunting—How, when, and where should hunting occur, while respecting tribal treaty rights and the concerns of other stakeholders?

Incorporated in these overarching issues is a broad spectrum of beliefs, concerns, and values held by a diverse range of stakeholders, including advocates, local community members, regulators and scientists, American Indian tribes, and the national and international public. Most of these constituents support the conservation of wild Yellowstone bison, but differ in their views regarding what constitutes conservation and responsible management actions to mitigate conflicts. The challenge for managers is to consider this wide variety of viewpoints and reach a reasonable solution for the long-term conservation of this ecologically important population, while accommodating the diverse policies and philosophies of various federal, state, and tribal agencies. In this chapter, we summarize key points pertinent to the conservation of Yellowstone bison and make recommendations for management in the near future.

## Key Points

Yellowstone Bison Are Migratory Wildlife, Not Livestock—A wild bison population can be defined as one that roams freely within a defined conservation area that is large and heterogeneous enough to sustain ecological processes such as migration and dispersal, has sufficient animals to mitigate the loss of existing genetic variation, and is subject to forces of natural selection (White and Wallen 2012; Bailey 2013). As demonstrated throughout this book, Yellowstone bison are exceptional at meeting these criteria. Wildlife species in Yellowstone National Park are not managed like domestic stock on a ranch and are generally allowed to move freely. However, while the park provides a large amount of habitat for bison and other wildlife, it does not encompass many of the lower-elevation winter ranges used by these animals when deep snow limits access to forage at higher elevations (Coughenour 2005; White et al. 2013b). As a result, some tolerance is necessary outside the park for wild bison to access resources for their survival—similar to the acceptance already provided to bears, bighorn sheep, deer, elk, moose, pronghorn, wolves, and other wildlife.

Brucellosis Will Remain in the Greater Yellowstone Area for the Foreseeable Future—As discussed in Chapter 2, the eradication or substantial suppression of brucellosis in wild bison and elk is not feasible at this time due to the absence of easily distributed and highly effective vaccines, limitations of current vaccine delivery technologies, potential adverse consequences such as injuries and changes in behavior from intrusive suppression activities, and chronic and increasing infection in elk distributed across more than 8 million hectares (20 million acres; U.S. Animal Health Association 2006; Cross et al. 2010; Treanor 2012; White et al. 2013c; USDI, NPS 2014). Therefore, brucellosis will remain endemic in the Greater Yellowstone Area for many decades to come.

Intensive Management of Yellowstone Bison Is Necessary at Times—Yellowstone bison will continue to move into Montana during winter, with more bison migrating as their numbers and winter severity increase (Geremia et al. 2011, 2014b). Due to existing agricultural and residential development, however, there is not sufficient low-elevation habitat in areas where bison are currently tolerated that could sustain many hundreds or thousands of animals for extended lengths of time. Thus, bison attempt to migrate further during some winters, including into areas occupied by hundreds of cattle. Also, bison will eventually attempt to pioneer new areas as their abundance increases, similar to


*Bison leaving the national park through the Roosevelt Arch near the northern boundary of Yellowstone National Park.*

the range expansion that occurred in the past (Taper et al. 2000; Plumb et al. 2009). When bison cross the park boundary into Montana their management is the prerogative of the state, including coordinated management with the Gallatin National Forest on National Forest System lands (16 USC § 1604). Montana has allowed several hundred bison to migrate outside Yellowstone National Park and occupy suitable winter range in the state—and tolerance on additional range may occur in the future (USDI, NPS et al. 2008; MFWP and MDOL 2012). However, mass migrations of bison have, at times, upset state and local governments and many private landowners and cattle operators (Montana Sixth Judicial Court, Park County 2013). If bison were allowed to disperse unimpeded into cattle-occupied areas of Montana, it is likely those bison would be lethally removed by state employees or during regulated hunts (U.S. District Court for the District of Montana, Missoula Division 2011). Also, the State might retract some tolerance for bison. Thus, management practices such as hunting, hazing, capture, and culling are necessary at times to limit the abundance and distribution of bison, while incrementally building acceptance for them in modern society (U.S. District Court for the District of Montana, Missoula Division 2011; see Chapter 10).

Yellowstone Bison Can Support Conservation and Cultural Practices Elsewhere—Yellowstone bison have high reproductive and survival rates for a wild population exposed to numerous predators and relatively severe environmental conditions (see Chapter 5). Thus, bison numbers increase rapidly when environmental conditions are suitable (see Chapter 3), which could quickly fill available habitat and out-pace acceptance for them in Montana. As a result, harvesting and culling bison is currently necessary at times to keep the limited tolerance for them in Montana from being rescinded (U.S. District Court for the District of Montana, Missoula Division 2011). Public and treaty harvests and the provision of meat from culled bison to tribes and food banks could improve cultural, economic, nutritional, and social well-being (see Chapter 9). Also, the use of quarantine to restore brucellosis-free Yellowstone bison to public and tribal lands would enhance the conservation of the species in North America.

## Recommendations for Future Management

Objectives—Biologists at Yellowstone National Park have recommended the following demographic, ecological, and genetic objectives for Yellowstone bison:

- Maintain 2,500 to 4,500 bison and average at least 3,000 to 4,000 over decades to preserve genetic diversity and reduce large-scale culls;
- Minimize the effects of selective culling on bison and allow numbers in the central and northern regions of the park to vary depending on dispersal rates and natural selection;
- Maintain similar proportions of males and females and an age structure of about 70 percent adults and 30 percent juveniles to facilitate competition for mates;
- Sustain ecological processes such as predation, migration, dispersal, and competition in the park and other agreed-upon conservation areas; and
- Restore the contributions of bison to herbivore-grassland dynamics, the predator-prey-scavenger association, and many other relationships in the ecosystem (Plumb et al. 2009; Gross et al. 2010; Pérez-Figueroa et al. 2012; White and Wallen 2012; Frank et al. 2013; Geremia et al. 2013; White et al. 2013c; Geremia et al. 2014a).

These objectives are consistent with the recommendations from recent reviews of ungulate management in national parks, but should be reassessed periodically based on new information and changed circumstances (Demarais et al. 2012). Hobbs et al. (2014) recommended managers use an adaptive management paradigm for Yellowstone bison, with the implementation of management actions for 3 to 5 years followed by assessments of progress, current knowledge and conditions, and updated model forecasts. Managers could then make an informed decision regarding how to proceed.

Brucellosis Containment—Given current technology and existing conditions, intrusive human actions such as vaccination or fertility control are unlikely to substantially decrease brucellosis infection in wild


*Bison calf in Yellowstone's Lamar Valley.*

bison and elk. If disease regulators want to suppress brucellosis in wildlife across the Greater Yellowstone Area, then they need to initiate a dialogue with all the stakeholders regarding what should be done based on various mandates, values, and viewpoints, and what can be done based on consideration of existing conditions and technologies, biological feasibility, and economic costs (Nishi 2010). In the meantime, the best alternative for suppressing brucellosis transmission is to maintain separation between bison, elk, and cattle during the transmission period from February to June (Keiter 1997; Bienen and Tabor 2006; Nishi 2010; Cross et al. 2013; Godfroid et al. 2013; Treanor et al. 2013; White et al. 2013c).

Tolerance—Allowing migratory bison to occupy public lands in Montana until most calving is completed by early June would reduce stress on pregnant or lactating females and newborn calves (Jones et al. 2010). It would also reduce the cost, duration, extent, and intensity of hazing needed to return bison to Yellowstone National Park each spring or early summer. This tolerance would not significantly increase the risk of brucellosis transmission to cattle because: (1) bison parturition is typically completed weeks before cattle occupy nearby ranges, (2) female bison consume most birthing tissues, (3) ultraviolet light and heat degrade *Brucella* bacteria on tissues, vegetation, and soil, (4) scavengers remove fetuses and remaining birth tissues, and (5) management maintains separation between bison and cattle (Jones et al. 2010; Schumaker et al. 2010; Aune et al. 2012; MFWP 2013).

One of the most vexing problems for the management of Yellowstone bison is the lack of available lower-elevation habitat in the Gardiner basin and southern Paradise Valley north of Yellowstone National Park. The valley bottoms in this area have more accessible forage and less snow than surrounding mountains during winter, but are already used for agricultural and residential development (Hansen 2009). As a result, up to 800 bison have been held in the Stephens Creek capture facility and other confinement pastures in and near Yellowstone National Park and fed hay for months during some winters to prevent their mass migration north of the park (White et al. 2011, 2013c). Confinement and feeding could unintentionally lead to food-conditioning, brucellosis transmission, and loss of migratory knowledge (Franke 2005; Gates et al. 2010; Bailey 2013; White et al. 2013c). Thus, managers should develop and emphasize management practices that avoid unnaturally concentrating bison during late winter, such as the enhancement and restoration of suitable forage plants in the Gardiner basin where unpalatable, noxious weeds have proliferated (Plumb et al. 2009; White et al. 2013c). Seasonal or year-round tolerance for wild bison should be attainable in some portions of the Greater Yellowstone Area where brucellosis transmission risk to cattle is low. Managers could use actions such as fencing, hazing, delaying cattle turn-on dates, and conservation easements or other incentives to maintain separation between bison and cattle during the transmission risk period (Kilpatrick et al. 2009). Federal and state wildlife agencies have acquired some grazing rights and key habitat for bison and other wildlife through agreements with willing landowners. They should continue to work with landowners to identify areas with suitable habitat for bison and develop strategies to resolve conflicts with livestock, human safety, and private property. These strategies could include agreements to promote heifers or steers on private lands and grazing allotments rather than cow-calf pairs. Also, managers should continue successful efforts to subsidize fencing in high-conflict areas and lower speed limits along highways crossed by bison. Nevertheless, human intervention will be necessary to manage groups of bison that approach geographic or social boundaries of tolerance. These efforts will likely require additional funding and staffing (MFWP and MDOL 2012).

Hunting—About 322 bison were harvested by public and treaty hunters during the winter of 2014, most of which were shot near the boundary of Yellowstone National Park and along roads. Increasing this harvest will require increased tolerance (e.g., year-round in some areas) for bison in Montana, better access for hunters, creative harvest strategies during non-traditional seasons, and commitments by hunters to adjust harvest methods in response to bison habitat use


*Bison near Officers' Row in Mammoth Hot Springs, Yellowstone National Park.*

patterns (White et al. 2011). State and tribal managers are discussing strategies that would allow bison to migrate into more dispersed areas across the landscape. They are also attempting to coordinate the overall harvest of bison by age, breeding area (central, northern), and sex. However, additional consultation is needed to effectively incorporate tribal subsistence hunts into current management strategies. Modern technology provides more efficient travel (vehicles), coordination (cell phones), gathering (rifles, winches), and long-term storage (freezers). As a result, tribal subsistence hunts to procure large amounts of meat appear unethical to some people in the complex and diverse social landscape surrounding Yellowstone National Park. Ongoing discussions are focusing on how to effectively support tribal treaty harvests, while respecting the concerns of other stakeholders about bison conservation, concentrations of gut piles near roads and residences, and human safety issues.

Hunting opportunities in Montana are limited in many years because most bison do not migrate outside Yellowstone National Park until March and April when public and tribal hunting seasons are closed due to females being late in pregnancy. As a result, the State of Montana and a few American Indian tribes have recommended hunting bison inside the park. Hunting in the park is not authorized by Congress and long-standing policy prohibits hunting in units of the National Park Service system unless specifically authorized by Congress (NPS Organic Act of 1916, 16 USC I, V § 26). Even if hunting were authorized, however, the National Park Service is opposed due to concerns about wounding, behavioral changes (avoidance), unintended effects to other iconic and sensitive wildlife species, and decreased wildlife viewing opportunities for visitors (Wenk 2012). Hunting just inside the park boundary would probably not be much more effective than hunting outside the park due to the late-winter and spring migration patterns of bison. Rather, hunting during autumn and early to mid-winter would be most feasible and effective in interior areas of the park (e.g., Blacktail Deer Plateau, Firehole and Madison river drainages, Hayden Valley, Lamar Valley) and away from roads. Even if these harvests were conducted by government agents or government-supervised hunters, they would almost certainly have unintended adverse effects to the bison population, other natural resources, and visitor enjoyment (Wenk 2012).

Nonetheless, there is a need for further consultation between the federal government and American Indian tribes associated with Yellowstone National Park to discuss recurring questions about potential hunting rights inside the park and whether Yellowstone bison should be managed as trust resources for the benefit of one or more specific tribes. One question is whether any tribes that signed treaties and land purchases/sales reserved the right to hunt bison within the park. To answer this question, it may be necessary to evaluate (1) whether the tribes understood the treaty agreements to mean that they retained the right to hunt in the ceded lands that now encompass Yellowstone National Park, and (2) whether Congress abolished these rights when it created the park in 1872 or passed the National Park Protective Act of 1894 that specifically prohibited hunting in the park (Molloy 2000). A separate question is whether the U.S. Department of the Interior has a trust responsibility to consult with tribes that have recognized treaty rights for hunting bison on open and unclaimed federal lands in Montana before removing Yellowstone bison to meat processing, research, or quarantine facilities. A few tribes have asserted that such removals could affect the number of bison available for harvest by tribal hunters because fewer bison will migrate outside the park (Whitman 2012; YNP 2012). Two related questions are: (1) should tribes with recognized treaty rights in Montana be preferentially provided with meat, hides, and other products from Yellowstone bison that are shipped to meat processing facilities over tribes that do not have treaty rights but are associated with Yellowstone National Park, and (2) should all brucellosis-free Yellowstone bison that complete quarantine be relocated to open and unclaimed federal lands in Montana where tribes with recognized treaty rights can hunt them (in lieu of relocating them elsewhere; YNP 2012)?

Capture and Culling—In some winters, several hundred bison may need to be captured and culled at boundary facilities to regulate population size (Geremia et al. 2013). Managers should cull animals in a non-selective manner to avoid potential adverse demographic and genetic consequences that could compromise population viability (Halbert et al. 2012; Treanor et al. 2013). Culling bison in proportion to their availability in the population may mimic natural mortality events and help maintain an age structure close to historical distributions—though aboriginal harvests from horseback may have disproportionately taken more females than bulls (Millspaugh et al. 2008; Clawson et al. 2013). Managers should avoid culling in a manner that artificially allows brucellosis or other factors to act as key selective forces (USDI, NPS and MFWP 2013).

If feasible, managers should implement smaller removals (25 to 50 bison) near the park boundary consistently through the migration season (Geremia et al. 2013). This stepwise approach would (1) limit bison held within capture facilities and minimize effects on hunting opportunities, (2) reduce logistical constraints of transporting large numbers of bison to meat processing facilities over brief periods, (3) avoid transporting females late in pregnancy to meat processing facilities, and (4) lower the chances of out-of-park migrations surpassing levels that exacerbate conflict (Geremia et al. 2013). If necessary, large removals of 500 or more bison could be implemented during severe winters and/or at high bison densities when large numbers of bison naturally migrate to lower elevations (Geremia et al. 2013).

Quarantine Facilities and Terminal Pastures—The ecological and adaptive value of Yellowstone bison merits efforts to relocate animals testing negative for brucellosis exposure to quarantine facilities for further testing and eventual release elsewhere (Treanor et al. 2013). Quarantine facilities could be paired with terminal pastures so any animals that test positive for brucellosis could be killed for food. These paired facilities could reduce the frequency of large shipments of bison to meat processing facilities when females are late in pregnancy, while enhancing bison conservation and the cultural heritage and nutrition of American Indian tribes. If necessary, pregnant bison could be held in terminal pastures through calving, with test-positive animals eventually killed and test-negative calves and other animals sent to quarantine. There is significant interest by federal and state agencies, American Indian tribes, non-governmental organizations, and private entities in receiving brucellosis-free Yellowstone bison and/or constructing and operating a quarantine facility on their lands (NPS, YNP and the Bureau of Indian Affairs 2012; Associated Press 2014). Also, the Department of the Interior recently identified 20 locations on federal lands within the historic range of plains bison that may be suitable for receiving Yellowstone bison completing quarantine (USDI 2014).

It is uncertain if periodically sending Yellowstone bison to quarantine will serve as a long-term tool for regulating the size of the population. The minimum quarantine periods and testing requirements are logistically difficult and relatively expensive to implement over several years (USDA, APHIS 2003; Clarke et al. 2014b). Also, there are substantial political and social hurdles to overcome in many areas. Thus, interest in obtaining Yellowstone bison is limited to groups that greatly value their cultural and evolutionary significance. In addition, recipients of brucellosis-free bison from quarantine could quickly reach saturation of their facilities and lands through subsequent breeding of these prolific animals. Thereafter, new herds formed from brucellosis-free Yellowstone bison would only need the occasional infusion of a small group of bison to enhance or maintain their existing genetic diversity. As a result, quarantine may not consistently remove large enough numbers of bison to regulate the size of the Yellowstone population.

Public Engagement—Most stakeholders are not satisfied with the level of involvement provided by the partners of the Interagency Bison Management Plan, which primarily amounts to comment periods at public meetings. Rather, stakeholders want substantive input into the decision-making process to influence management strategies before they are adopted and implemented. As a result, managers should consider alternate forms of public involvement such as stakeholder workshops with presentations and discussion that allow information and ideas to be transferred and deliberated between managers, scientists, and the public (Bidwell 2010; Berger and Cain 2014). Management committees comprised of all interested stakeholders could be formed and sustained to develop ideas and recommendations similar to the Citizens Working Group on Yellowstone Bison (2011) and the model used for managing the Book Cliffs and Henry Mountains populations (Utah Department of Natural Resources 2014).

*A wild bison population can be defined as one that roams freely within a defined conservation area that is large and heterogeneous enough to sustain ecological processes such as migration and dispersal, has sufficient animals to mitigate the loss of existing genetic variation, and is subject to forces of natural selection.*

Scientific monitoring and research has greatly increased knowledge regarding bison, brucellosis, and elk in the Greater Yellowstone Area. Gaining this knowledge was a critical step for bison conservation, but also highlighted that human dimensions have a large influence on policy changes when it comes to tolerance for large wildlife such as bison outside national parks and refuges (Berger and Cain 2014). Therefore, additional information is needed on political and socioeconomic factors such as: (1) comparative costs and public preferences for various management alternatives, (2) non-market values of wild bison, (3) the demand for bison removed from the population, (4) traditional knowledge from American Indians and local communities, and (5) public attitudes, behaviors, and knowledge of bison, brucellosis, and management (Nishi 2010; National Research Council 2013). Also, public confidence in decisions could be enhanced by soliciting independent reviews of analyses and proposed plans, as well as meeting with local officials to gain their input, and hopefully, support (National Research Council 2013; Berger and Cain 2014).

## Conclusions

The overriding issue regarding the conservation of Yellowstone bison and plains bison elsewhere in North America is whether the public will support wild bison living outside preserves (Lott 2002; Franke 2005; Bailey 2013). Arguments against tolerance for Yellowstone bison, or their restoration elsewhere, are generally presented in terms of disease, protection of property, and human safety concerns—even though elk have similar effects yet are tolerated without intrusive management because they are economically valuable for hunting. However, there are also underlying issues about grass (i.e., competition with cattle), political control (i.e., state versus federal rights), and the continuing transition of communities from traditional rural occupations and lifestyles such as ranching to tourism and the enjoyment of natural amenities (i.e., locals versus outsiders; Haggerty and Travis 2006; Bailey 2013). While these characterizations are overly simplistic, disease regulators and livestock interests have certainly perpetuated misperceptions regarding the risks posed by bison for decades (Robbins 2006; Bidwell 2010). Even today, these misperceptions strongly influence the management of bison and severely limit their conservation and distribution across the landscape (Bidwell 2010).

The reluctance to allow Yellowstone bison onto more public lands in the Greater Yellowstone Area can no longer be justified solely based on brucellosis risk to the cattle industry. There is recognition by both disease regulators and wildlife managers that the risk of brucellosis transmission from bison to cattle is minute compared to elk which are generally free to roam (Bienen and Tabor 2006; Kilpatrick et al. 2009; Schumaker et al. 2010). Also, the economic consequences of occasional brucellosis outbreaks in cattle are greatly reduced since the Animal and Plant Health Inspection Service changed its regulations in 2010 to deal with outbreaks on a case-by-case (rather than state-wide) basis, and designated surveillance areas for brucellosis were established (USDA, APHIS 2010; MDOL 2013). Despite several detected transmissions of brucellosis from elk to cattle, the gross annual income from cattle sales in Montana surpassed $1 billion six times during 2005 to 2013, with record-high cattle prices since 2010 (Lutey 2012, 2013). Furthermore, studies in Wyoming have clearly demonstrated that the costs of measures to prevent brucellosis transmission from elk to cattle are exorbitant compared to the costs of an occasional outbreak in cattle (Roberts et al. 2012; Kauffman et al. 2013).

Current conditions in the Greater Yellowstone Area present an opportunity to manage bison similar to other wildlife in some areas outside national parks and refuges. Tourism and recreational activities have a large and growing influence on the economy, and the vast majority of visitors and hunters to the area enjoy seeing bison move across the greater landscape in large numbers. In fact, the Yellowstone area provides a unique attraction—the opportunity to see bighorn sheep, bison, deer, elk, pronghorn, and large predators such as bears and wolves in close proximity on the landscape and within view from paved roadways. Furthermore, American Indian tribes have become more engaged with the management of bison in the area, sharing their traditional knowledge, restoring bison to tribal lands, and renewing subsistence hunts to improve their cultural, nutritional, and social well-being (Plumb and Sucec 2006; Hatfield et al. 2013). As a result, efforts to respect the presence of bison as wildlife on the larger landscape will be welcomed by native peoples and the majority of the local, national, and international public. This vision is attainable because decades of management have shown there are relatively few conflicts between bison, residents, and the millions of visitors each year in Grand Teton and Yellowstone national parks. Acceptance of bison as wildlife in some areas outside parks and refuges will enhance bison restoration, enrich visitor experience, improve public and treaty hunting opportunities, boost local and state economies, and hopefully, elicit regional and national pride in this tremendous conservation accomplishment. The time is right to recover bison, the iconic symbol of power and strength in our nation, as wildlife in appropriate locations of the Greater Yellowstone Area and elsewhere.


*Bull bison in summer in Yellowstone National Park.*


*Bison calves with new horns
in Yellowstone National Park.*

# Acknowledgments

Special thanks to the following scientists for sharing their time and expertise reviewing a draft version of this book:

Steve Cain, Grand Teton National Park, National Park Service; Curtis Freese, Freese Consulting, Westport, Massachusetts; Dan Licht, Midwest Region, National Park Service; John Nishi, EcoBorealis Consulting, Inc., Canada; Wes Olson, Grasslands National Park, Parks Canada (retired); Glen Sargeant, Northern Prairie Wildlife Research Center, U.S. Geological Survey; and Dirk Van Vuren, Wildlife, Fish, and Conservation Biology, University of California, Davis.

We also thank the Yellowstone Association for financial support to produce both printed and electronic versions of this book; Sarah Garrott, Executive Editor of Oregon Law Review, for guidance regarding the interpretation of American Indian treaty rights; and Robert Garrott, Montana State University, for allowing us to use unpublished data on the causes of bison mortality.

Thanks also to Jim Peaco and Neal Herbert of the National Park Service and Michael Nichols of the National Geographic Society for taking many of the photographs used in this book.

The views and opinions in this book are those of the authors and should not be construed to represent any views, determinations, or policies of the National Park Service.


*Bison feeding near the Blacktail Deer Plateau in Yellowstone National Park.*

# Glossary of Terms[9]

**Acquired immunity:** Immunity gained through prior exposure to a disease, vaccination, or some other manner than heredity.

**Adaptive capabilities:** Ability to adapt to a changing environment.

**Adaptive management:** A repetitive decision-making process that includes: (1) describing the problem and desired outcomes, (2) modeling the system, (3) predicting the effects of management actions, (4) implementing management actions, (5) monitoring to evaluate the effectiveness of actions, and (6) making adjustments based on learning to enhance progress.

**Allele:** Alternative forms of a gene at a specific site (locus) on a chromosome.

**Allelic diversity:** The total number of possible alleles at each gene locus in a population.

**Amenity living:** Residing in a place that is comfortable, convenient, and/or pleasing.

**Analytic deliberation:** Engaging stakeholders to discuss the technical aspects, human dimensions (e.g., beliefs, values), and trade-offs of various management alternatives; followed by recommendations to decision makers.

9 Portions of this glossary were adapted from USDI, NPS (2010, 2014). References are provided in the text.

**Antibody:** A protein molecule produced after exposure to an infectious disease that can combine with the disease organism.

**Apparent competition:** The rate of predation on a given prey species is influenced by the presence of another prey species that allows the predator to survive and reproduce at higher numbers than could be sustained by one prey species alone.

**ATP:** Adenosine-5´-triphosphate which is produced by oxidative phosphorylation in mitochondria and transports chemical energy within cells for metabolism.

**Bacteria:** Unicellular microorganisms of the class Schizomycetes.

**Bio-absorbable projectile:** Remote delivery device where vaccine is encapsulated into a bullet-like capsule that dissolves in liquid.

**Birth:** The process of bearing offspring, which is also known as parturition.

**Bison management area:** A zone where some bison are tolerated for part or all of the year without increasing the risk of brucellosis transmission to cattle.

**Body condition:** The state of fat and protein stores in an animal that reflects nutritional intake and deposition or metabolism based on their physiological requirements and environmental conditions.

**Bovine/Bovinae:** The subfamily of animals that includes bison, cattle, oxen, European buffalo, water buffalo, and yaks.

**Breeding herd:** An aggregation of animals for breeding.

***Brucella abortus*:** A species of bacteria that functions as a parasite within cells to cause bovine brucellosis in bison, cattle, and elk.

**Brucellosis:** An infectious disease of cattle, dogs, goats, and pigs that is caused by *Brucella* bacteria and can induce abortions in animals and recurring (undulant) fever in humans.

**Buffalo:** Name commonly used to refer to bison.

**Carnivore:** Meat eater.

**Carrion:** Tissues of dead animals.

**Carrying capacity:** The number of animals that can be supported in a given area based on the limits of available food, space, and other resources.

**Cattle:** Domesticated animals of the family Bovidae (bison, cows, oxen) that are kept on a farm or ranch.

**Cell-mediated (or cellular) immune response:** The activation of phagocytes, T-lymphocytes, and cytokines within cells in response to disease-causing organisms.

**Cellulose:** Fibrous material that comprises the walls of plant cells.

**Chromosome:** A single piece of coiled DNA that contains many genes.

**Competition:** A direct or indirect interaction with another animal decreases the ability of an animal to survive and reproduce.

**Confederated Salish and Kootenai Tribes of the Flathead Nation:** The Bitterroot Salish, Kootenai, and Pend d'Oreilles tribes that currently live on the Flathead Reservation in northwestern Montana.

**Conservation:** The preservation and stewardship of natural resources and the ecological processes that sustain them.

**Contraception:** A method of preventing fertilization or pregnancy.

**Copulate:** Sexual intercourse.

**Culling:** The removal of animals from a population for management purposes.

**Culture (disease tests):** A method for detecting or increasing bacterial or viral organisms in a test sample.

**Culture-negative:** A culture test result that did not detect the organism of interest in a sample.

**Culture-positive:** A culture test result that detects the organism of interest in a sample.

**Decomposers:** Organisms that break down dead or decaying matter.

**Demography:** Statistics relating to births, deaths, emigration, and immigration.

**Density:** The number of animals in a defined area.

**Density-dependent:** A response that occurs when there are a high number of animals within a given area.

**Diagnostics:** Procedures for detecting and/or identifying a disease.

**Digestible energy:** The portion of food that can be absorbed to provide energy to an animal.

**Disease:** An impairment of normal physiological function in part or all of an animal.

**Dispersal:** Movement to another area without returning shortly thereafter.

**DNA:** Deoxyribonucleic acid which contains genetic instructions for the development and functioning of animals.

**Domestic (animal):** A farm animal or pet that is not wild.

**Dose:** A prescribed amount of vaccine.

**Ecological role:** The relationships and interactions among animals and their environment.

**Ecology:** The study of relationships among organisms and their environment.

**Efficacy:** Effectiveness at producing a desired result.

**Emigration:** The movement of animals out of a population or area.

**Endemic (disease):** Sustained in an area or population without being brought in from outside sources.

**Energetics:** The movement and transformation of energy.

**Epidemiology:** The study of factors and mechanisms involved in the spread of a disease.

**Epizootic:** An outbreak of disease that spreads quickly among animals and could be transmitted to humans.

**Euro-Americans:** Americans with ancestry in Europe.

**Exotic:** Nonnative or introduced from a foreign place.

**Extinction:** A group of related organisms dies out.

**Extirpation:** Destroyed or wiped out.

**Experimental challenge:** The deliberate introduction of an infectious disease organism into a controlled environment.

**Fecundity:** The ability to produce offspring.

**Fertility control:** Devices or methods used to prevent fertilization or pregnancy.

**Fetal:** Related to a fetus.

**Fetus:** An unborn, developing mammal.

**Fidelity:** *See* Philopatry.

**Field strain:** A type of disease organism found in the wildland environment.

**Foraging:** Searching for and ingesting food.

**Forbs:** Broad-leaved, herbaceous plants.

**Foreign cells:** Cells uncharacteristic of the organism.

**Founder effect:** The loss of genetic variation when a new population is established by a small number of individuals from a larger population.

**Free-ranging:** *See* Wide-ranging.

**Gene:** The basic unit of heredity (inheritance) which consists of DNA that contains instructions to make proteins.

**Gene flow:** The transfer of genes (alleles) from one population to another.

**Gene pool:** The set of all genes in a population.

**Generation time:** The approximate time it takes individuals to replace themselves in a population, or in other words, the time between two successive generations (about 8 to 10 years in Yellowstone bison).

**Genetic diversity:** Variation of heritable characteristics in a population which allows some animals to adapt to a changing environment.

**Genetic drift:** A change in the frequency of alleles in a population due to chance or random events rather than natural selection.

**Genetic integrity:** The preservation of existing genetic diversity and substructure.

**Genetics:** The study of heredity.

**Genetic subdivision/substructure:** *See* Population subdivision.

**Genotypes:** Genetic make-ups of individual animals.

**Geothermal:** Heat from the earth that flows to the surface and produces hydrothermal features (e.g., geysers, hot springs, fumaroles, mud pots) in some areas, while warming more extensive portions of the landscape and reducing or eliminating snow pack.

**Gestation:** Time of pregnancy.

**Grass-like plants:** Rushes and sedges.

**Grazing:** Consume vegetation.

**Grazing optimization:** The production of grasses is increased by grazing and the cropping of vegetation.

**Greater Yellowstone Area:** The general area surrounding Yellowstone and Grand Teton national parks where the states of Idaho, Montana, and Wyoming share a boundary (about 400 kilometers north-to-south and 200 kilometers east-to-west).

**Green-up (of vegetation):** Commencement and continuation of new growth by live green plants.

**Group defense:** Animals in a group cooperate to protect themselves and their young.

**Habitat:** The environment in which an animal lives that includes cover, food, space, water, and other resources necessary for an animal to survive and reproduce.

**Haplotype:** Segments of DNA that are transmitted together and contain closely linked gene variations.

**Harvest:** *See* Hunting.

**Hazing (of bison):** People with equipment moving animals away from a location where they are not wanted.

**Herbaceous:** Plants without woody stems that die after each growing season.

**Herbivore:** Plant eater.

**Herd:** A group of animals from the same species that feed, travel, and interact together for a period of time.

**Heredity:** Inheritance or the genetic transfer of traits to offspring.

**Heterogeneity:** Diversity or variation.

**Heterozygosity:** An index of genetic diversity that sums the proportion of genes with different alleles (alternative forms of a gene) across a representative sample of a population.

**Hoof:** Horny covering of the feet of animals such as bison, cattle, and elk (plural is hooves).

**Horning:** Rubbing horns against an object such as a tree or shrub.

**Horns:** One or more projections from animal's head that consist of a sheath of hardened protein covering bone.

**Hunting:** Pursuing an animal to kill it for food (subsistence), sport, and/or spiritual or cultural reasons.

**Husbandry:** The care and protection of animals in a manner similar to livestock.

**Immigration:** Movement of animals into a population or area.

**Immune protection:** Resistance to a disease-causing organism that may be natural (i.e., inherited) or acquired (e.g., vaccination).

**Immune response:** A bodily response that involves the recognition of disease organisms by specific antibodies in blood, previously sensitized lymphocytes, and/or phagocytes, T-lymphocytes, and cytokines within cells.

**Immunity:** The ability of an organism to defend itself against an infectious disease.

**Immunocontraception:** The stimulation of an animal's immune system to cause infertility.

**Inbreeding:** Reproduction between individuals that are closely related that often produces offspring with deleterious traits.

**Indigenous:** Originating from or belonging to a particular region or place.

**Infection:** The invasion of, and proliferation within, an animal's body by disease-causing microorganisms such as bacteria, viruses, and parasites.

**Infectious disease:** Diseases caused by infectious bacteria, viruses, fungi, protozoa, and helminthes.

**Infectious dose:** The amount of disease-causing organism that stimulates an infection.

**Inheritance:** Traits transmitted from parents to their offspring through genes.

**Interagency Bison Management Plan:** A plan signed in 2000 between the State of Montana and the federal government that prescribed collaborative actions to reduce the risk of brucellosis transmission from Yellowstone bison to cattle, while conserving a wild population of bison with some migration to lower-elevation winter ranges on public lands in the state.

**InterTribal Buffalo Council:** A federally chartered organization established in 1990 to restore bison to tribal lands.

**Intracellular pathogens:** Disease-causing organisms that operate inside cells.

**Introgression:** Hybridization or the introduction of genes from one species into the gene pool of another species.

**Lactation:** The production of milk by female mammals.

**Latent disease:** A disease characterized by periods of inactivity either before symptoms appear or between attacks.

**Litigation:** A lawsuit brought in court to assert or defend a particular right.

**Livestock:** Domesticated animals raised on farms or ranches for food and other products.

**Locus:** Specific location of a gene (DNA sequence) on a chromosome (plural is loci).

**Lymph node:** An organ that is a part of the lymphatic (immune) system and contains white blood cells that trap foreign particles.

**Lymphatic system:** A bodily system that transports lymph through tissues and organs for immune protection.

**Lymphocyte cells (T-cells):** Leukocytes (white blood cells) found in large numbers in lymph tissues that contribute to immunity.

**Management (wildlife):** The conservation of populations of wild animals and the ecological processes that sustain them, while considering other biological, economic, political, and social factors.

**Meat processing facility:** A facility where animals are killed and their meat and other parts are packaged and/or distributed.

**Metabolic rate:** The amount of energy expended by an animal during a certain time period.

**Metabolism:** The chemical processes that convert food into energy and other products necessary to sustain life.

**Metabolizable energy:** The amount of nutrients in food that can be absorbed by an animal for energy.

**Microsatellite DNA:** Repeating sequences of DNA that result from a mixing of DNA from both parents.

**Migration:** Seasonal, round-trip movements between separate areas not used at other times of the year.

**Mitochondrial DNA:** Genetic information that is normally inherited exclusively from the mother.

**Mortality:** Death or death rate.

**Mutation:** A change in a gene or chromosome that can produce an inherited trait.

**Native peoples:** Indigenous people that have certain inherent rights based on their original occupation of an area.

**Natural immunity/resistance:** Ability to resist a disease due to inherited traits.

**Natural selection:** Animals with traits that make them better suited to the environment tend to survive, reproduce, and transmit their genetic characteristics to succeeding generations more than other animals.

**Nez Perce Tribe:** An American Indian tribe that currently governs and lives within its reservation in Idaho.

**Nitrogen cycling:** The process by which nitrogen is converted into one or more chemical forms that can be used by plants for photosynthesis and growth.

**Nitrogen mineralization:** The process by which microbes convert proteins and other chemical compounds in organic matter into forms that can be used by plants such as ammonium and nitrate.

**Numerical dilution:** The likelihood of an individual animal being eaten decreases as the number of available prey animals increases.

**Nutrients:** Chemical substances in foods that enable animals to survive and reproduce.

**Nutrition:** The process of ingesting and using food substances.

**Nutritional condition:** *See* Body condition.

**Nutritive quality:** The amount of energy and nutrients in food.

**Open and unclaimed federal lands:** Public land in the United States that is not being used in a manner inconsistent with tribal hunting. Yellowstone National Park is not considered open and unclaimed land because it exists to preserve native wildlife and hunting is prohibited. National Forest System lands are considered open and unclaimed lands. Private property is not considered open and unclaimed land.

**Organic matter:** The remains (carcasses) of dead plants and animals or their waste products (feces, urine).

**Organism:** A life form (e.g., animal, bacteria, plant) composed of interdependent parts that maintain vital processes.

**Ovulation:** The release of ripe eggs from the female ovary.

**Parasite:** An organism that lives in or on an animal and benefits at its expense.

**Parturition:** The process of giving birth.

**Pathogen:** Anything that causes disease such as a bacteria, virus, or other microorganism.

**Phenology (of vegetation):** Periodic life cycle events (e.g., leaf, bud, flower, and seed formation) that are influenced by seasonal and interannual variations in weather and other factors such as elevation.

**Philopatry:** Tendency to stay in, or return to, a given area.

**Physiology:** The study of how cells, muscles, and organs work together in animals.

**Placenta:** The organ in the womb to which the fetus is attached.

**Plains bison:** One subspecies of American bison (the other subspecies is the wood bison [*Bison bison athabascae*]).

**Population:** A collection of individuals of the same species that live in the same area and interbreed.

**Population bottleneck:** A drastic, temporary reduction in the number of animals in a population.

**Population dynamics:** Changes in the size and composition (age, sex) of populations, and the factors and processes influencing those changes.

**Population subdivision/substructure:** Relatively independent subsets or separate groups within a population.

**Predation:** An interaction in which one organism (the predator) attacks and feeds on another (the prey).

**Pregnancy:** Female animal carrying one or more fetuses in her body from fertilization to birth.

**Prevalence:** The number of cases of a disease.

**Productivity (wildlife):** The number of young produced in a population.

**Pyric herbivory:** Preferential grazing of burned patches that reduces the likelihood of fires in the near future and promotes a shifting pattern of disturbance across the landscape that supports a variety of plants and animals.

**Quarantine (bison):** Animals are maintained in fenced enclosures separate from other livestock and wildlife for a period of time while they are repeatedly tested to evaluate if they remain free of brucellosis.

**Radio collar:** *See* Radio telemetry.

**Radio telemetry (wildlife):** The transmission of information (e.g., direction, location) from a transmitter attached to an animal to a receiver where the information can be processed or downloaded.

**Range expansion:** The outward dispersal of animals beyond the limits of the traditional distribution for a population.

**Recruitment:** The number of young that survive to enter a population in a given year.

**Reintroduction:** *See* Restoration.

**Remote delivery (vaccination):** Method of delivering a biological product such as a vaccine without physically capturing and restraining individual animals.

**Removals (of bison):** The culling or harvest of animals from a population.

**Reproduction:** Procreation or the process of creating new offspring.

**Reproductive success:** Breeding and passing on genes to the next generation.

**Reproductive synchrony:** The birth of most offspring in a population within a short period of time each year.

**Resistance (disease):** Immunity or the ability of an animal to repel infection from a disease.

**Resources (natural):** A naturally occurring material that could be used by humans or wildlife.

**Restoration:** The return of something that was removed or nearly extirpated.

**Riparian areas:** Zones on or adjacent to rivers and streams that are typically inhabited by a diversity of animals and plants.

**Rumen:** The first compartment of the four-chambered stomach of ruminants.

**Ruminants:** Animals with a four-chambered stomach that includes microorganisms such as bacteria and protozoa to break down plant material into volatile fatty acids and other compounds.

**Ruminate:** Regurgitating partially digested food and chewing it again to further break down plant material.

**Scale:** The size of measurements at which ecological processes are studied, including the area, number, duration, and frequency of sampling (large-scale generally refers to observations over relatively long periods of time or extensive areas of space).

**Scavengers:** Animals that feed on dead or injured animals.

**Select agent:** Biological agents and toxins that could be packaged as weapons by terrorists and used to threaten public health or national security (www.selectagents.gov).

**Senescent:** Vegetation that has aged past maturity and is becoming old and dying.

**Serology:** Tests to detect the presence of antibodies against a disease organism in the blood serum (plasma).

**Seronegative:** The absence of specific antibodies in blood serum for a particular disease.

**Seropositive:** The presence of specific antibodies in blood serum that indicate past exposure to a particular disease.

**Seroprevalence:** The proportion of a population that has been exposed to a disease as determined by the presence of antibodies in the blood.

**Shed:** To discharge from the body.

**Shipment (of bison):** The capture and transport of animals to meat processing facilities, quarantine facilities, terminal pastures, research facilities, or another location.

**Simulation (computer):** A program that attempts to replicate a model of a particular system.

**Slaughter:** *See* Meat processing facility.

**Social tolerance:** *See* Tolerance.

**Species:** A group of populations that contain individuals that resemble each other and can interbreed.

**Stakeholders:** People and organizations that use, influence, and/or have an interest (or stake) in a given resource.

**Summer range:** The geographical area or region within which a population or species can be found during summer.

**Survival:** Continuing to live.

**Susceptible:** Not currently, but capable, of being affected or infected by a disease.

**T-cells:** Leukocytes (white blood cells) found in large numbers in lymph tissues that contribute to immunity.

**Terminal pasture:** Fenced enclosure in which bison are maintained separate from other livestock and wildlife, and harvested by shooting or transfer to a meat processing facility.

**Test-and-slaughter:** Animals are captured, tested for exposure and/or infection with a particular disease such as brucellosis, and killed or otherwise removed from the population if they test positive. Animals that test negative are often vaccinated for the disease and released.

**Thermal:** *See* Geothermal.

**Tolerance:** Acceptance of some animal or thing.

**Transmission (disease):** The passage or transfer of an infectious disease from one individual to another.

**Treaty rights:** Rights reserved by American Indian tribes through treaties with the U.S. government that can include hunting, gathering, or conducting other activities on certain "open and unclaimed" federal lands.

**Trust responsibility:** An obligation of the U.S. government to protect tribal assets, lands, resources, and treaty rights.

**Ungulates:** Hooved mammals such as members of the orders Perissodactyla (horses, rhinos, and tapirs) and Artiodactyla (pigs, camels, deer, antelope, cattle, and their kin).

**Utilization distribution:** A probability distribution derived from data identifying the locations of one or more animals at different points in space and time.

**Vaccination:** Administration of vaccine to stimulate a protective immune response against an infectious disease.

**Vaccine:** A suspension of living or inactivated organisms used to induce a protective immune response against an infectious disease.

**Variation in male reproductive success:** Many males successfully breeding and passing their genes on to the next generation (as opposed to one or a few males monopolizing breeding—which could lead to a loss of genetic diversity).

**Vegetation:** Plants.

**Virus:** A submicroscopic, parasitic microorganism composed of nucleic acid (DNA or RNA) inside a protein covering.

**Wallowing:** A behavior when bison roll to give themselves a dust bath, and in the process, create depressions in the soil.

**Weaning:** A mother stops nursing (milk) her offspring so it will begin eating other foods.

**White blood cells:** B-cells, T-cells, macrophages, monocytes, and granulocytes in the immune system that circulate in the blood and lymph and participate in defensive reactions to invading microorganisms or foreign particles.

**Wide-ranging:** Animals move across a vast landscape rather than being confined to a feedlot or enclosure.

**Wild (bison):** A population that roams freely within a defined conservation area that is large and heterogeneous enough to sustain ecological processes such as migration and dispersal, has sufficient animals to mitigate the loss of existing genetic variation, and is subject to forces of natural selection such as predation, substantial environmental variability, and competition for breeding opportunities and food.

**Wildlife:** Wild animals, birds, and other living things.

**Windthrow:** The uprooting, breakage, or toppling of trees by wind.

**Winter-kill:** Starvation.

**Winter range:** The geographical area or region within which a population (or part thereof) is found during winter.

**Yearling:** An animal between one and two years of age.

**Yellowstone bison:** Bison that primarily live in Yellowstone National Park, but sometimes migrate to lower-elevation ranges in surrounding states during winter and spring.

**Yellowstone National Park:** The world's first national park established in 1872 and located on 2.2 million acres in the states of Idaho, Montana, and Wyoming.


*Bison in Yellowstone National Park.*

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*A group of bison near Soda Butte Creek in the northeastern region of Yellowstone National Park.*

# Index

The iconic bison deserves our best efforts to assure its place on the American landscape. I am grateful to the authors for clearly articulating the issues we face as we collectively determine the future of these animals. The authors have given us a chance to advance our discussions based on a common understanding of the science, culture, and politics surrounding bison.

— From the Preface by Daniel N. Wenk

ISBN 978-0-934948-30-2
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